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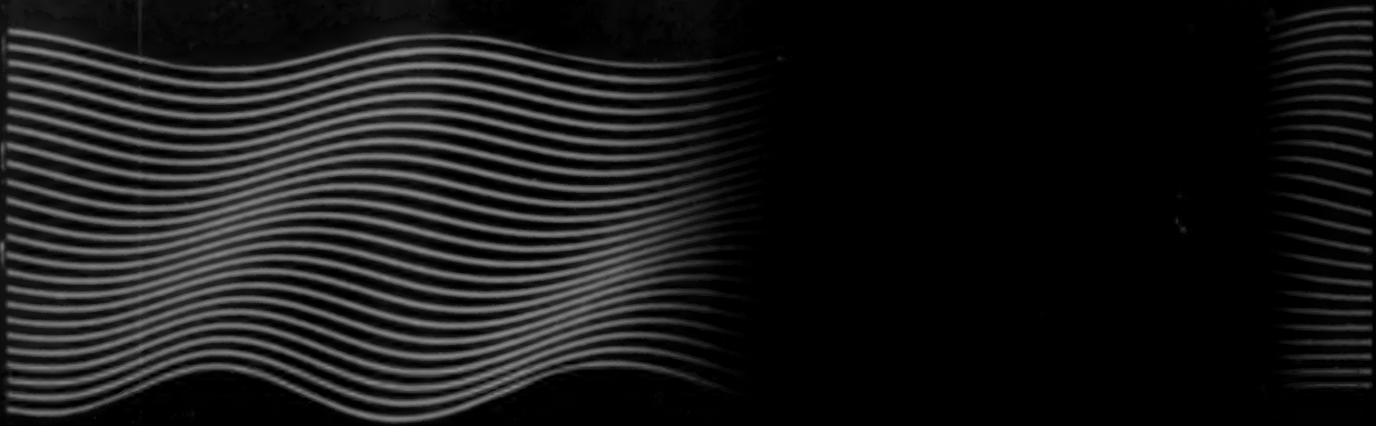

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Separating genetic and environmental influences on temporal spawning distributions of largemouth bass (*Micropterus salmoides*)

Mark W. Rogers, Micheal S. Allen, and Wesley F. Porak

Abstract: Environmental and genetic factors influence fish spawning periodicity (i.e., the distribution of spawning events during the breeding season), but their relative contributions have rarely been evaluated. We evaluated the relative contribution of genetic and environmental effects on spawning periodicity by rearing Florida largemouth bass (FLMB, *Micropterus salmoides floridanus*) from Lake Okeechobee and intergrade largemouth bass (ILMB, *Micropterus salmoides salmoides* × *M. s. floridanus*) from Lake Seminole in a similar environment. Fish from each genetic source population were translocated to experimental ponds at an intermediate latitude in Gainesville, Florida, in September 2003. We used estimated ages of offspring as an index of spawning events to compare spawning distributions between brood sources in ponds and related those results to spawning distributions at source populations for 2004. FLMB began spawning earlier than ILMB in all ponds, and FLMB had a longer spawning season than ILMB. Similarly, FLMB at Lake Okeechobee began spawning earlier and had a longer spawning season than ILMB at Lake Seminole. Environmental factors (e.g., temperature effects) influenced spawning periodicity for both FLMB and ILMB, but spawning periodicity was also influenced by genetic composition in ponds because translocated fish reflected characteristics of their source populations. Thus, both environmental factors and genetic composition influenced spawning periodicity.

Résumé : Les facteurs environnementaux et génétiques influencent la périodicité de fraye (c'est-à-dire la répartition des événements de fraye au cours de la saison de reproduction), mais leurs contributions relatives ont rarement été évaluées. Nous avons déterminé les contributions relatives des effets génétiques et environnementaux sur la périodicité de fraye en élevant des achigans à grande bouche de Floride (FLMB, *Micropterus salmoides floridanus*) du lac Okeechobee et des formes variantes de l'achigan à grande bouche (ILMB, *Micropterus salmoides salmoides* × *M. s. floridanus*) provenant d'un environnement similaire au lac Seminole. Nous avons transféré des poissons de chaque population-source génétique dans des étangs expérimentaux à une latitude intermédiaire à Gainesville, Floride, en septembre 2003. Nous avons utilisé les âges estimés des rejetons comme indice des événements de fraye afin de comparer la répartition de la fraye chez les reproducteurs des deux origines dans les étangs et de relier ces résultats aux répartitions de la fraye dans les populations sources en 2004. Les achigans à grande bouche de Floride commencent à frayer plus tôt que les ILMB dans tous les étangs et les FLMB ont une saison de reproduction plus longue que celle des ILMB. De même, les FLMB au lac Okeechobee commencent à frayer plus tôt et ont une saison de fraye plus longue que les ILMB au lac Seminole. Les facteurs environnementaux (par ex., les effets thermiques) influencent la périodicité de la fraye chez les FLMB et les ILMB, mais la périodicité de la fraye est aussi affectée par la composition génétique dans les étangs parce que les poissons transférés reflètent les caractéristiques de leur population source. Ainsi, tant les facteurs environnementaux que la composition génétique affectent la périodicité de la fraye.

[Traduit par la Rédaction]

Introduction

Genetic and environmental factors influence fish spawning periodicity (i.e., the distribution of spawning events during the breeding season), but their relative contributions are often difficult to discern. Many studies (e.g., Ludsin and DeVries 1997; Garvey et al. 1998) have illustrated the importance of hatching (i.e., early- versus late-hatched fish in a year class) to growth and survival of age-0 fishes, but few have evaluated the factors influencing spawning periodicity. Spawning initiation (i.e., the onset of the breeding season) is regulated by environmental factors such as temperature and photoperiod (Kramer and Smith 1960; Lam 1983), and thus, spawning seasons occur later in the year at high latitudes

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relative to low latitudes (Conover 1992). Spawning season duration is often inversely related to latitude, in part because adults cease spawning when offspring no longer have a chance for overwinter survival (Johannes 1978; Munro et al. 1990; Conover 1992). Spawning periodicity has been related to multiple environmental factors, such as water temperature (Conover 1992), photoperiod (Heidinger 1975), changes in water levels (Ozen and Noble 2002), and food availability during gonadal development (Koslowski 1992). For example, Atlantic cod (*Gadus morhua*) in the Baltic Sea delayed spawning during years of cooler spring water temperatures (Wieland et al. 2000). Largemouth bass (*Micropterus salmoides*) began spawning in a Puerto Rico reservoir, which was thermally stable (24–30 °C) through the year, when photoperiod began to increase during winter (Ozen and Noble 2005). Spawning duration was also related to water level fluctuations in Puerto Rico reservoirs (Ozen and Noble 2002).

Genetic composition of a stock also influences spawning periodicity. Reproductive processes in fish are regulated, in part, by endogenous hormone cues (Patiño 1997; Van Der Kraak et al. 1998), which are regulated by genes (e.g., Denslow et al. 2001). Genotypic effects have led to synchronous spawning of predators in relation to prey abundance, thus resulting in high availability of food resources for newly hatched larvae, assuming increased foraging opportunities at hatching leads to increased survival for offspring (Hjort 1914; Cushing 1975). Atlantic herring (*Clupea harengus harengus*) exhibit genotypic influences to spawning periodicity across their broad latitudinal range because hatching within specific larval retention areas is related to increased local food availability (i.e., plankton blooms) for larvae in that specific locale (Cushing 1975; Sinclair and Tremblay 1984). Similarly, genetics can influence spawning periodicity because evolution of multiple spawning or a prolonged spawning season may prevent loss of an individual's annual reproductive output because of environmental conditions (Conover 1992; Fox and Crivelli 1998). However, the relative contributions of genetic and environmental influences are poorly understood, and variable spawning initiation and periodicity are often attributed to phenotypic plasticity (Baylis et al. 1993; Conover and Schultz 1997). Contributions of genotypic variability to phenotypic patterns have largely been ignored (Conover and Schultz 1997).

Largemouth bass provide an excellent species for evaluating genetic and environmental influences on spawning periodicity because they have a wide native geographic distribution with a natural genetic gradient, as indicated by latitudinal clines in allele frequencies at several loci (Philipp et al. 1983). Ecologically, juvenile largemouth bass suffer from differing mortality factors across latitudes (Garvey et al. 1998), and spawning periodicity strongly influences juvenile largemouth bass survival and recruitment (Ludsin and DeVries 1997; Pine et al. 2000). Thus, differing selection pressures may exist along the latitudinal distribution of largemouth bass that would facilitate localized adaptations for spawning periodicity. Comparisons among genetically verified fish indicated that northern largemouth bass (NLMB, *Micropterus salmoides salmoides*) spawned earlier than Florida largemouth bass (FLMB, *Micropterus salmoides floridanus*) and intergrade largemouth bass (ILMB, *M. s. salmoides* × *M. s. floridanus*) when stocked together in Illinois ponds and a Texas reservoir (Isely et al. 1987; Maceina et al. 1988), but those studies occurred outside the native range of FLMB. No studies have separated environmental influences on spawning periodicity from genetic influences by comparing populations with known genetic contrasts while monitoring environmental conditions.

Genetic differences across the distribution of largemouth bass have been recognized for decades. NLMB and FLMB have been recognized as distinct subspecies for more than 50 years (Bailey and Hubbs 1949). NLMB are endemic to the northern United States, FLMB naturally occur in south Florida, and ILMB occur in north Florida, several southeastern states (e.g., Georgia, Alabama, Mississippi, South Carolina, North Carolina, Virginia, and Maryland), and other areas where introductions have occurred. Kassler et al. (2002) recommended elevating the status of FLMB from a subspecies to species status (i.e., Florida bass, *Micropterus floridanus*) based on discriminant function analysis of meristic characters, allozyme analysis, and mitochondrial DNA (mtDNA) data. Physiological attributes (e.g., temperature tolerances) and relative survival differences have also been reported for translocated fish in several performance evaluations (e.g., Cichra et al. 1982; Philipp and Whitt 1991). However, phenotypic variability in morphometric and life history traits of broadly distributed species is not uncommon (Schultz et al. 1996). At the time of our study, the taxonomic nomenclature accepted by the American Fisheries Society remains at the subspecies level.

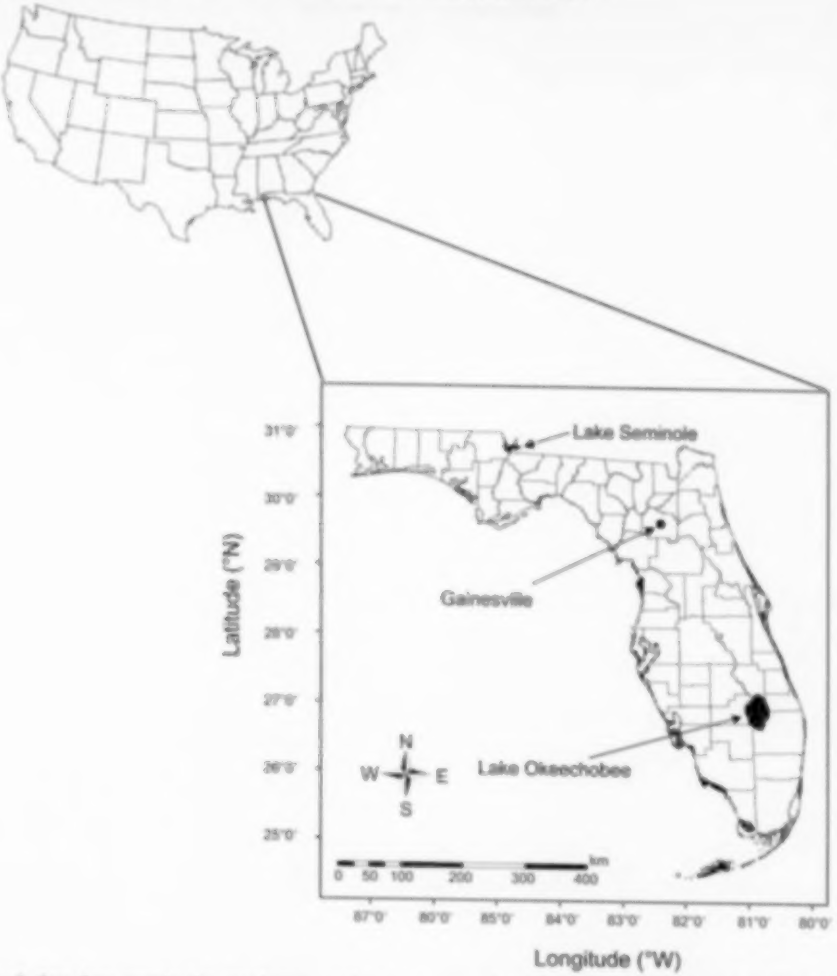
We compared temporal hatching distributions between a population of FLMB from Lake Okeechobee in south Florida and an ILMB population from Lake Seminole at the Florida–Georgia border. Lake Okeechobee represents a pure population of FLMB, and Lake Seminole is an intergrade population (Philipp et al. 1983). We used estimated hatch dates from sagittal otoliths as indices of spawning periodicity assuming that hatching occurred 2 days after fertilization. Spawning periodicity was compared between brood sources for fish reared in environmentally similar experimental ponds at an intermediate latitude. We also assessed whether the trends found in experimental ponds corresponded to the spawning periodicity for the two natural populations at their source lakes. Our study design allowed us to maintain similar environmental conditions during brood fish sexual maturation at the intermediate latitude and evaluate influences of genetic factors to spawning periodicity. If genetic composition affected spawning periodicity, we expected spawning of translocated fish to reflect the periodicity of their source populations. In contrast, we surmised that if environmental factors more strongly influenced spawning periodicity, then translocated fish that spawned in ponds would have similar distributions, and pond distributions would differ from both source-lake populations.

Materials and methods

Pond methods

Brood largemouth bass were captured by electrofishing at Lake Okeechobee, Florida (latitude: 27°7′N), and Lake Seminole, Florida (latitude: 30°44′N), during September 2003 (Fig. 1). Using brood fish from Lakes Okeechobee and Seminole allowed us to nearly encompass the maximum latitudinal

Fig. 1. Locations for Lake Seminole, Lake Okeechobee, and Gainesville, Florida, USA.



distance in Florida and, therefore, nearly the maximum environmental gradient (i.e., temperature and photoperiod) acting as selective pressures on spawning periodicity. Philipp et al. (1983) observed clinal variation in allele frequencies at several loci in largemouth bass that had been collected from Lake Seminole in north Florida down to Lake Okeechobee. Philipp et al. (1983) failed to detect NLMB alleles at Lake Okeechobee and estimated a subspecific NLMB:FLMB genomic presence of 49:51 at Lake Seminole based on electrophoresis of two diagnostic enzyme loci. Recent analyses at the same loci also detected no northern alleles at Lake Okeechobee and indicated that largemouth bass at Lake Seminole were highly introgressed and had likely been introgressed for an extended time period (B.L. Barthel, Illinois Natural History Survey, 1816 South Oak Street, Champaign, IL 61820, unpublished data). Analyses of mtDNA and allozyme data have resulted in Lakes Seminole and Okeechobee being grouped into separate largemouth bass genetic conservation management units within Florida (B.L. Barthel, unpublished data).

Brood stock from source populations were size-selected within 300–430 mm total length (TL) so that fish were of a reproductively mature size (Chew 1974) and to avoid influences of brood fish size on spawning periodicity (Miranda and Muncy 1987; Goodgame and Miranda 1993). Adult fish were transported to Gainesville, Florida (latitude: 29°43′N), using an aerated 2 m × 3 m fish transport tank within 24 h of capture (Fig. 1).

We stocked six experimental ponds in Gainesville, Florida, with brood fish. Ponds approximately measured 25 m × 5 m, with an average maximum depth of 1 m, and were parallel to each other with a 3 m levee separating each pond. One week prior to stocking, the ponds were treated with rotenone (5% liquid rotenone; >3 mg·L^{-1}), drained to ensure no fish remained, and then refilled. Each pond was randomly assigned 10–11 brood stock from a single lake (N = 3 replicates per brood source) assuming a similar sex ratio for each group (Chew 1974). Brood fish were fed 90–110 mm (TL) golden shiners (*Notemogonus chrysoleucas*) at 3.5% of largemouth bass biomass per day (Miranda and Hubbard 1994) until spawning behavior was observed in spring. Aquatic vegetation in ponds was maintained at a minimum using manual removal, but removals were ceased when largemouth bass spawning bed construction was first

Table 1. Earliest, median, and latest hatch dates of Florida (Lake Okeechobee fish) and intergrade (Lake Seminole fish) largemouth bass (*Micropterus salmoides*) translocated to experimental ponds at Gainesville, Florida, in 2004 and corresponding mean water temperatures.

			Estimated hatch date				Water temperature (°C) at hatch date		
Source	Pond	N^a	Earliest	Median	Latest	Hatch range (days)	Earliest	Median	Latest
Okeechobee	A	30	26 Jan.	2 Apr.	7 Apr.	72	12.4	18.2	18.6
	B	40	1 Feb.	29 Feb.	9 Mar.	37	12.3	12.3	18.4
	C	41	12 Feb.	21 Feb.	7 Mar.	24	15.1	15.4	22.6
Seminole	D	40	7 Mar.	12 Mar.	18 Mar.	11	17.7	14.2	17.7
	E	40	22 Feb.	27 Feb.	5 Mar.	12	15.7	14.0	19.6
	F	40	6 Mar.	11 Mar.	16 Mar.	10	20.6	16.0	19.4

[a] N = number aged.

observed to prevent disturbance of spawning activity. Pond water levels were maintained at bank-full to avoid influences of water level on timing of bass spawning (Sammons et al. 1999; Ozen and Noble 2002). Water temperature was measured four times daily in each pond, at 1 m depth, using remote temperature recorders (Onset Incorporated). Age-0 fish were collected during April and May using dip nets and electrofishing. Rotenone was also used during the May sample to maximize the likelihood that all sizes and ages of age-0 largemouth bass were collected from each pond. The experiment was terminated in May 2004 to reduce potential effects of cannibalism and high water temperatures on age-0 largemouth bass and to avoid increased maintenance because of rapid evaporation.

Field methods

Hatching dates at source lakes were estimated using age-0 largemouth bass captured at Lake Okeechobee during February, April, and June 2004 and at Lake Seminole during May and July 2004. The earlier trip at Lake Okeechobee was conducted because of the potential for early hatching at low latitudes (Gran 1995). Age-0 largemouth bass were collected using 10 m × 10 m block nets and applying rotenone at 3 mg·L^{-1}. Twelve block nets were set at each lake during each sampling event, and fish were collected using dip nets by wading investigators.

Laboratory analyses

A subsample of age-0 largemouth bass from experimental ponds and source lakes were size-selected for age estimation so that the age sample mirrored the length–frequency of the fish collected at each water body (Pine et al. 2000). Selected age-0 largemouth bass were measured (TL; mm) and weighed (wet weight; 0.001 g), and their sagittal otoliths were removed. Sagittal otoliths were prepared using the methods of Miller and Storck (1982). Each otolith was read by two independent readers, and ages were averaged when they agreed within 3 days between readers. If agreement was not met, the otolith was reread by both readers and discarded if agreement was not met ($N = 0$ for pond fish). Some early-hatched age-0 fish from source populations were too old (>150 days) for reliable age estimation in July, but we assumed their hatch dates were represented in samples collected earlier in the year (i.e., February or April–May). Median hatch date in ponds was compared between stocking sources using a nonparametric median test (Zar 1999). Mean hatch date, mean water temperature at first and median hatch date, and mean hatching duration in ponds were compared between broodstock sources using one-way analysis of variance (ANOVA). Quantitative comparisons between pond and source lake spawning distributions were not performed because of differences in parental size distributions. However, source lake spawning patterns were used to evaluate whether spawning periodicity observed in ponds was similar to source populations in their native environment.

Results

Several largemouth bass nests ($N \geq 3 \cdot \text{pond}^{-1}$), with guarding males, were observed in each pond, and age-0 bass were captured in all six experimental ponds. Female largemouth bass may use multiple nests and deposit multiple egg clutches during a spawning season (Heidinger 1975), thus we assumed that bass progeny in our experimental ponds represented offspring from several families. About 20 age-0 bass were selected for age estimation from each pond during each sample. Age estimates were only made for 30 age-0 bass from pond A (Lake Okeechobee brood stock) because of a low sample size ($N \cong 25$) and small TL distribution during April. The low sample size in April was likely due to a high mortality event because all fish collected were <25 mm, except one individual was 32 days older and much larger than any other fish in that sample.

In ponds, FLMB had initial hatching dates beginning as early as 26 January and as late as 12 February (Table 1; Fig. 2). In contrast, the range of initial hatch dates was 22 February to 7 March for ILMB (Table 1; Fig. 2). On average, median hatch date in ponds was 11 days earlier for FLMB than for ILMB ($\chi^2 = 31.22$, df = 1, $P < 0.001$), and mean hatch date in ponds was 5 days earlier for FLMB ($F = 5.10$, $P = 0.025$) (Table 1). FLMB began spawning at cooler water temperatures (12.3–15.1 °C) than ILMB (15.7–20.6 °C) in experimental ponds ($F = 7.82$, df = 4, $P = 0.049$), but water temperatures at median hatch date did not differ between brood types ($F = 0.010$, df = 4, $P = 0.771$) (Table 1). Hatching duration in experimental ponds ranged 24–72 days for FLMB and 10–12 days for ILMB (Table 1). FLMB hatching duration was marginally different than ILMB hatching duration ($F = 5.40$, df = 4, $P = 0.08$), but low statistical power ($N = 3 \cdot \text{treatment}^{-1}$) reduced our ability to detect a difference

Fig. 2. Five-day cohort percent hatching distribution (*y* axis) for age-0 largemouth bass (*Micropterus salmoides*) hatched in research ponds at Gainesville, Florida, across dates (*x* axis) and corresponding mean water temperatures (*z* axis). Sampling occurred on 15 April and 10 May 2004. Left column (*a*–*c*, representing Ponds A–C, respectively): brood source was Lake Okeechobee; right column (*d*–*f*, representing Ponds D–F, respectively): brood source was Lake Seminole.

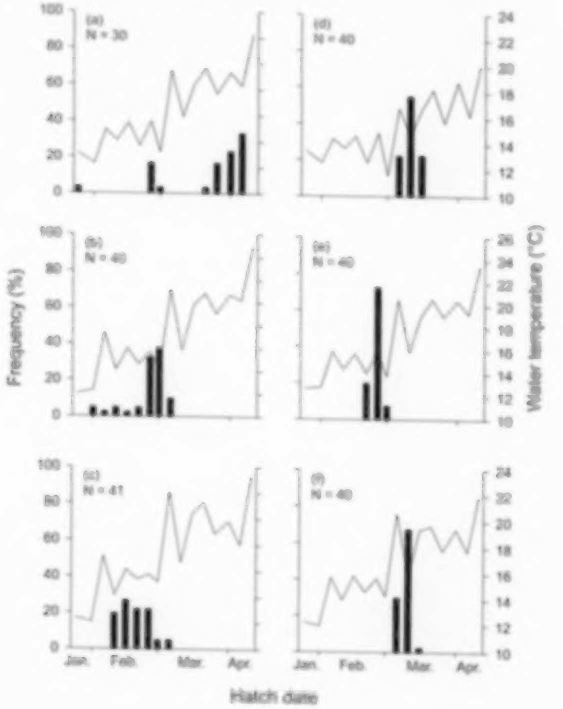
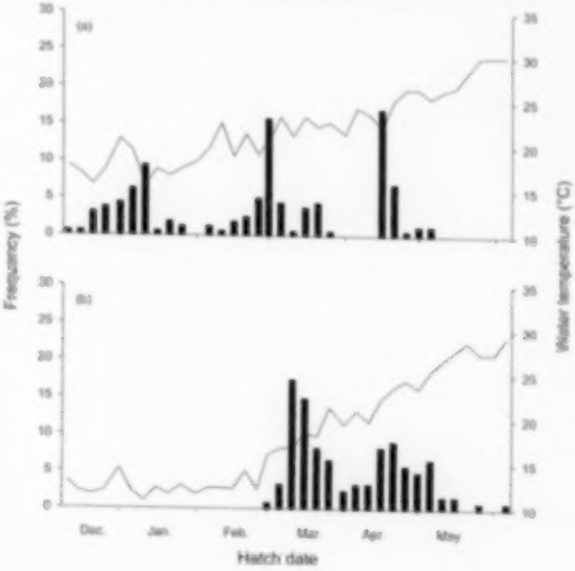


Fig. 3. Five-day cohort percent hatching distribution (*y* axis) for age-0 largemouth bass (*Micropterus salmoides*) collected at Lakes (*a*) Okeechobee ($N = 159$) and (*b*) Seminole ($N = 121$) across dates (*x* axis) and corresponding mean water temperatures (*z* axis). Sampling occurred at Lake Okeechobee on 15–16 February, 22 April, and 21–22 June 2004. Sampling occurred at Lake Seminole on 12–13 May and 13–14 July 2004.



(Peterman 1990). FLMB hatching occurred as late as 7 April, whereas the last ILMB hatch occurred on 18 March in experimental ponds. FLMB began spawning earlier and also had a longer spawning season than ILMB in experimental ponds.

Our experimental pond results were corroborated by data from Lakes Okeechobee and Seminole. Age-0 bass at Lake Okeechobee began hatching as early as 12 December, whereas the earliest fish collected from Lake Seminole hatched on March 1 (Fig. 3). The median hatch date at Lake Okeechobee occurred 29 days earlier than the median hatch date at Lake Seminole. Unlike our pond results, water temperatures at first hatch were similar between source lakes (Lake Okeechobee = 17.9 °C; Lake Seminole = 16.3 °C), and water temperatures at median hatch date were similar (Lake Okeechobee = 19.6 °C; Lake Seminole = 20.9 °C), as seen in our pond study. Hatching duration results also supported experimental pond results because Lake Okeechobee hatching duration (146 days) was substantially longer than the Lake Seminole hatching duration (97 days) (Fig. 3). In summary, FLMB had earlier spawning and longer spawning season duration than ILMB in both research ponds and at their respective source lakes.

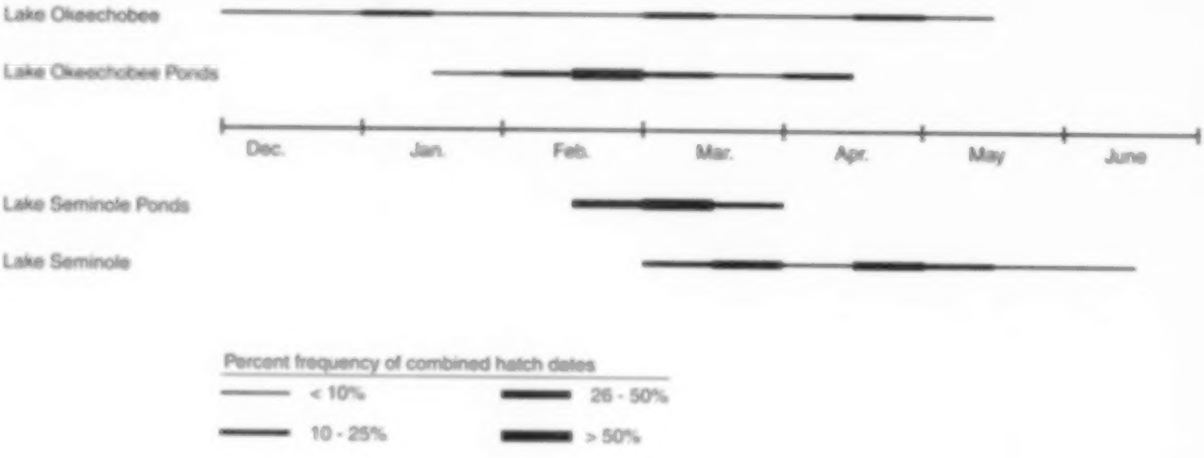
Our results indicated both environmental and genetic effects on spawning periodicity of largemouth bass. Translocation illustrated environmental effects on hatching periodicity because rearing FLMB in research ponds at a higher latitude led to later hatching than at Lake Okeechobee. Similarly, rearing ILMB in research ponds at a lower latitude led to earlier hatching in ponds than at Lake Seminole (Fig. 4). Genetic effects on hatching periodicity were also evident because translocated fish reflected characteristics of their brood source populations. For example, FLMB hatched earlier and had longer hatching distributions than ILMB in both the pond experiment and at brood source lakes (Fig. 4).

Relative differences in spawning times between brood sources in ponds were detected despite the low number of families and adult sizes represented by our pond brood fish relative to source lake populations. Although our intent was to compare relative differences between brood sources in ponds, source lake hatching patterns mirrored our pond results, providing further support for a genetic contribution to spawning periodicity. This corroboration occurred even though our brood fish samples were not representative of the entire spawning population from the source lakes (i.e., lower range in brood fish size in ponds compared with lakes).

Discussion

Environmental and genetic factors influenced spawning timing and periodicity of translocated largemouth bass. Environmental and genetic effects to breeding periodicity have rarely been investigated, but have been shown in some cases for terrestrial (e.g., Japanese macaques, *Macaca*

Fig. 4. Semimonthly hatching distributions for age-0 largemouth bass (*Micropterus salmoides*) reared in research ponds in Gainesville, Florida, and in-source populations at Lake Seminole and Lake Okeechobee in 2004. Figure lines are weighted to represent percent frequency.



fuscata; Fooden and Aimi 2003) and aquatic species (e.g., Atlantic salmon, *Salmo salar*; Donaghy and Verspoor 1997). For example, Atlantic salmon exhibited a reversal in hatching order between two populations when reared in a hatchery versus their native rivers (Donaghy and Verspoor 1997). Donaghy and Verspoor (1997) attributed the reversal in hatching order to a genotype–environmental interaction; although they could not explain the mechanism leading to the reversal, they suggested that local genetic adaptations to water temperatures were responsible. Environmental influences were evident by a temporal shift in the onset of spawning for translocated brood fish. In our research ponds, FLMB began spawning later than their source population did at Lake Okeechobee, which is located much farther south. In contrast, ILMB in research ponds began spawning before their source population at Lake Seminole, which is further north. Water temperatures were the most plausible explanation for observed temporal shifts because temperatures at median hatch date were similar between FLMB and ILMB in experimental ponds and field collections, but similar patterns in ponds and source lakes suggested a genetic component to spawning periodicity.

Genetic factors played a role in spawning timing because FLMB from Lake Okeechobee spawned earlier in the research ponds than ILMB from Lake Seminole, even though temperatures, photoperiod, and water levels were similar in all ponds during brood fish sexual maturation and spawning. Adaptations for reproductive strategies that maximize individual fitness via offspring survival and reproductive success should occur within an environment given a heritable component and selection pressure on phenotypic variability (Endler 1986). Einum and Fleming (2000) documented a "critical episode of selection" following the emergence of Atlantic salmon fry, which resulted in a phenotypic shift towards earlier emergence. A heritable component to breeding date has been established for some salmonids (Siitonen and Gall 1989; Gharrett and Smoker 1993), thus Einum and Fleming (2000) concluded that local adaptations for breeding dates are possible and may explain the variability in breeding dates within and among Atlantic salmon populations. The evidence of a genetic component to breeding times in our study and other studies is not surprising given that local populations of fishes, with restricted gene flow, have an underappreciated capacity to adapt to local selection (Conover and Schultz 1997).

In our study, FLMB exhibited protracted spawning periods in both ponds and lakes relative to ILMB. Protracted spawning distributions increase the likelihood that individuals with differing hatching dates will experience differing environmental conditions (Narimatsu and Munehara 1999). Mild winter water temperatures that typically occur in peninsular Florida likely prevent exposure of early-hatched fish to very cold temperatures (<12 °C) that would limit survival, as per Philipp et al. (1985). Atypical winter cold fronts can reduce growth or survival of early-hatched largemouth bass at Lake Okeechobee, thus reproductive success may vary among years for early- versus late-hatched fish. Garvey et al. (2002) found a similar pattern for bluegill (*Lepomis macrochirus*) at Lake Opinicon, Ontario, and hypothesized that protracted spawning distributions maximized lifetime fitness in variable environments where temperature regulates juvenile survival. Conversely, early spawning (e.g., in December) of largemouth bass at Lake Seminole would likely result in very limited offspring survival. Lake Seminole fish began spawning at suitable temperatures in March and spawned over a relatively shorter period compared with Lake Okeechobee fish. A contracted spawning distribution at Lake Seminole maximizes the growing season for most age-0 bass (e.g., Conover 1992) at the more northern latitude. Contracted spawning seasons for ILMB at Lake Seminole could be the result of stabilizing selection, where progeny from both early and late hatching times are at a survival disadvantage, which ultimately leads to individuals adapted to spawning within a shorter time period (Schultz 1993). Protracted spawning distributions of Lake Okeechobee fish and contracted spawning distributions of Lake Seminole fish appear better suited for the environments found at each source lake and inherent environmental influences on juvenile survival.

Philipp et al. (1985) found a lower α threshold temperature (i.e., the theoretical lower limit to embryonic development) for FLMB than for ILMB. Philipp et al. (1985) hypothesized that NLMB evolved strategies that delay spawning to prevent exposure of embryos to lethally cold temperatures, whereas FLMB evolved to allow spawning at lower and higher temperatures relative to NLMB. Our results support this hypothesis, and we conclude that largemouth bass spawning seasons are locally adapted to environmental conditions.

Natural selection may also lead to spawning periodicity that is synchronized with prey species abundance to maximize food availability for progeny (Sinclair and Tremblay 1984). The relationship between reproductive timing and food supply has been described by the "match/mismatch hypothesis", which asserts that temperate fishes spawn at a fixed time corresponding to peaks in plankton production, and offspring success or survival depends on how well their production matches with food production (Cushing 1975, 1990). At Lake Okeechobee, prey fish likely spawn earlier than at Lake Seminole because of earlier spring warming. Earlier hatching of fish at Lake Okeechobee, relative to hatching times at more northern latitudes, may lead to increased survival because of a size advantage relative to prey fish, which is a prerequisite for piscivory (Mittelbach and Persson 1998). Potential prey fish at low latitudes commonly have extended spawning seasons (Conover 1992) (e.g., mummichog, *Fundulus heteroclitus*; Conover 1990) relative to spawning seasons at more northern latitudes. Thus, differences in spawning periodicity we observed may have resulted from selection for optimal environmental conditions, food availability, or a combination of these factors.

Previous studies comparing spawning timing of largemouth bass indicated that NLMB and ILMB hatched earlier and at cooler water temperatures than FLMB (Isely et al. 1987; Maceina et al. 1988), which is contrary to our findings. These previous comparisons were conducted in Illinois and Texas, respectively, which are outside the native range of FLMB and have much cooler winter water temperatures than FLMB experience in their native range. Our pond study was conducted in a transition zone where both pure FLMB and ILMB populations naturally occur (Philipp et al. 1983), so brood fish were reared in temperatures that did not vary as widely from local conditions compared with Isely et al. (1987) and Maceina et al. (1988). Isely et al. (1987) and Maceina et al. (1988) also used sympatric populations of NLMB and FLMB, potentially allowing for confounding effects of hormonal cues and (or) reproductive behaviors, which may have influenced spawning times. We used separate ponds for each genetic source to prevent interbreeding and behavioral influences between brood source types. Broodstock lengths may have also contributed to differing results among studies because larger largemouth bass have been shown to spawn earlier than smaller individuals (Goodgame and Miranda 1993), and a large range in length distribution of spawning bass likely leads to extended spawning activities (Miranda and Muncy 1987). In our study, we used similar-sized brood stock from both sources to minimize potential size effects on spawning in ponds. Adult size distributions in ponds did not reflect adult size distributions at source lakes, thus we focused our comparisons of spawning distributions between ponds and used lake spawning periodicities to evaluate the relative differences. Adult size structures did not drastically differ between source lakes (M.W. Rogers, unpublished data), thus fish size effects on spawning periodicity were probably similar for both source populations. We standardized brood fish size in ponds, and spawning periodicity trends were similar to lake populations for each source, providing further evidence of a genetic component to spawning periodicity.

Comparisons of spawning periodicity using otoliths only reveal data for survivors and not the true distribution if age- or size-selective mortality occurs (Miller and Storck 1984; Isely et al. 1987). Our analyses only allowed for comparisons of surviving offspring between brood sources, which is the main concern for management and conservation purposes, but fish that hatched and incurred high short-term mortality had lower detection probability in our study. Sample timing is important to our results because differing mortality among ponds could have biased spawning periodicity results, especially if sensitivities to mortality factors differed by source. For example, FLMB are less tolerant of cold temperatures than ILMB (Williamson and Carmichael 1990; Philipp and Whitt 1991). We found only one individual in one of the Lake Okeechobee broodstock experimental ponds that was hatched in January, suggesting a high mortality event. Our median hatch date results for Lake Okeechobee experimental fish would not have differed without capturing the early-hatched individual, but the spawning duration for that pond would have been shorter. Our age-0 fish from both ponds and lakes were in the range of 13–73 days and 18–136 days, respectively, which provided a valid assessment of relative spawning times between sources. Interpretation of our results should consider potential biases of sample timing on combined spawning distributions. Fish hatched prior to April collections were potentially available for collection during both samples, which would shift median estimates to earlier in the year. In contrast, early-hatched fish also endured mortality factors for a longer time period relative to later-hatched fish, which could potentially shift our estimated spawning distributions towards later in the year. Lastly, termination of our experiment in mid-May could have led to an underrepresentation of fish that would have hatched later; however, we detected no hatching during the 30-day period prior to ending the experiment, suggesting that our data represent the entire spawning distributions. In summary, comparisons of our results with future studies should consider the time of collection for age-0 fish and potential influences on the apparent spawning distributions.

Environmental experiences of brood fish prior to relocation may persist and confound apparent genetic effects in common environment studies (Conover and Schultz 1997). Earlier spawning of FLMB could be partially due to environmental influences prior to relocation if FLMB were further in their annual reproduction cycle and gamete development was more advanced than ILMB when they were translocated. We stocked brood fish into experimental ponds in mid-September when such effects should have been minimized. Gross et al. (2002) reported that plasma sex steroid concentrations were low for male and female FLMB in September for fish reared at Gainesville, Florida, in their study. Increased gonadosomatic index of FLMB reared in Gainesville, Florida, began in November and peaked in February–March, which was strongly correlated with gonadal maturation (Gross et al. 2002). We translocated brood fish at least 3 months before spawning occurred at either lake. A future study utilizing progeny of translocated fish would further reveal genetic influences on spawning periodicity. Transplanting studies are useful for evaluating the genetic basis of phenotypic variation in spawning periodicity, but the genetic component we identified suggests further need to test and develop hypotheses to determine natural selection processes responsible for observed differences (Conover and Schultz 1997).

An important consideration when interpreting our study results is that our fish were only from two lakes, thus we did not have a random sample of FLMB or ILMB genotypes. Recent genetic studies concluded that our source populations were from differing genetic conservation management units (B.L. Barthel, unpublished data); however, we did not include brood fish from a range of lakes for each genetic conservation unit.

Our study has implications to management decisions regarding fish stocking programs. Outbreeding depression effects (e.g., lower recruitment, adult abundance, and fish size structure) of stocking FLMB with native LMB populations have not been reported throughout a widely distributed range of public water bodies stocked in the United States. However, Gharrett et al. (1999) reported outbreeding depression in the F_2 generation of pink salmon (*Oncorhynchus gorbuscha*) that were hybrids of stocks with distinctly different breeding seasons and warned that deleterious effects of outbreeding depression may take decades to detect. In a series of common garden experiments, Philipp et al. (2002) concluded that hybridization of largemouth bass from widely separate geographic locations (e.g., Florida, Illinois, Texas, and Wisconsin) with native Illinois fish led to a more than a 50% reduction in reproductive fitness relative to the original, local stock. Our study did not address individual- or population-level effects of mixing ILMB and FLMB, but genetic factors played a role in spawning timing and periodicity of translocated largemouth bass. Observed spawning periodicity appeared to be better suited for, and a local adaptation to, the environments found at each source lake. Genetic variation among local populations is likely prevalent (Conover and Schultz 1997), therefore we recommend that agencies take a conservative approach in stocking programs to avoid potential outbreeding depression. We also recommend that agencies develop long-term studies that evaluate effects of mixing stocks with phenotypic differences in life history strategies.

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A comparison of species assemblages between drainage systems with and without floodgates: implications for coastal floodplain management

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Abstract: Coastal floodplains provide essential nursery habitat for a large number of fish and prawn species, many of which are commercially and recreationally important. Human activities in coastal floodplains, such as those associated with agriculture and (or) development, can have detrimental impacts on this nursery function. We examined the potential role of flood mitigation structures, in particular tidal floodgates, in depleting estuarine and inshore fisheries stocks in eastern Australia. We compared species assemblages (abundance and biomass) in reference and gated drainage systems in the Clarence River floodplain (New South Wales, Australia) over a 1-year period. We subsequently determined which environmental variables were associated with the observed patterns in species assemblages. Our results show that abundance, biomass, and assemblages of juvenile fishes and invertebrates differed significantly and consistently between drainage systems with and without floodgates. The major environmental variables of concern in systems with floodgates were (*i*) presence of a floodgate, (*ii*) elevated concentrations of nutrients, and (*iii*) abundance of aquatic weeds. We discuss our findings in light of potential strategies to improve coastal floodplain management for fisheries production purposes.

Résumé : Les plaines de débordement côtières servent d'habitat essentiel de nursery pour un grand nombre d'espèces de poissons et de crevettes, dont plusieurs ont une importance commerciale ou sportive. Les activités humaines dans les plaines de débordement, telles que celles reliées à l'agriculture et (ou) au développement, peuvent avoir des impacts négatifs sur cette fonction de nursery. Nous examinons le rôle potentiel des structures de mitigation des inondations, en particulier des vannes de marée, dans la réduction des stocks de poissons commerciaux dans les estuaires et les eaux intérieures de l'est de l'Australie. Nous avons comparé les groupes d'espèces (abondance et biomasse) dans des bassins versants témoins et d'autres munis de vannes dans la plaine de débordement de la Clarence (Nouvelle-Galles du Sud, Australie) durant 1 année. Nous avons ensuite identifié les variables du milieu associées aux patterns observés dans les regroupements d'espèces. Nos résultats montrent que l'abondance, la biomasse et les regroupements de jeunes poissons et d'invertébrés diffèrent de manière significative et régulière entre les bassins versants avec et sans vannes. Les principales variables environnementales à surveiller dans les systèmes munis de vannes sont (*i*) la présence de vannes, (*ii*) les concentrations élevées de nutriments et (*iii*) l'abondance de plantes aquatiques nuisibles. Nous discutons de nos résultats dans le contexte des stratégies possibles pour améliorer la gestion des plaines de débordement côtières afin de favoriser la production des pêches commerciales.

[Traduit par la Rédaction]

Introduction

Aquatic habitats in coastal floodplains are a vital component in the maintenance of tropical and subtropical estuarine and inshore fisheries stocks (Blaber 2000). Many of the more important fisheries species use a number of coastal floodplain habitats in succession during their ontogenetic development (Gilanders et al. 2003). Hence, the protection and restoration of the range of habitats found in these areas, rather than a single key or critical habitat, is an issue receiving increasing prominence from fisheries scientists and managers (Cowx and Welcomme 1998; Gilanders et al. 2003).

Coastal floodplains worldwide are under pressure from continued concentration of human populations in coastal regions. As a result, coastal floodplains are subjected to altered hydrological regimes, agricultural and urban develop-

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ment, introduction of alien species, unsustainable harvest of native species, and declines in water quality (Bildstein et al. 1991). These impacts affect aquatic habitats in coastal floodplains and threaten fish and fisheries production (Brazner and Beals 1997; Beck et al. 2001).

In Australia, the major threats to the aquatic habitats in coastal floodplain habitats are (*i*) land and water management practices associated with grazing and intensive cultivation and (*ii*) the increasing residential and industrial development near urban centres (Cappo et al. 1998). For example, since the 1950s, extensive flood mitigation schemes, including levee banks, drainage channels, floodgates, dams, and weirs, have been constructed along the eastern coast to control floodwaters (Cappo et al. 1998). In contrast with their intended use, these structures are often operated as complete barriers to restrict saltwater inflow and tidal exchange, allowing use of land previously unsuitable for grazing and intensive cultivation (primarily sugarcane, *Saccharum* spp.) (State Pollution Control Commission (SPCC) 1978). These management and development practices have various impacts on fisheries stocks, the two most important ones being (*i*) modification and alienation of important aquatic habitat areas (Morton 1992; Pollard and Hannan 1994; Gibbs et al. 1999) and (*ii*) drainage of acid sulfate soils (Callinan et al. 1996).

Artificial drainage of coastal floodplains has resulted in losses of various types of aquatic habitats (Cappo et al. 1998). Moreover, flood mitigation and drainage structures prevent tidal access, thereby reducing water quality (SPCC 1978, 1987), promoting growth of aquatic weeds (SPCC 1978; Cappo et al. 1998), and blocking fish passage for migration and dispersal (Pollard and Hannan 1994; Halls et al. 1998, 1999). Consequently, the construction of flood mitigation schemes is likely to affect population genetics and dynamics of fisheries species, including stock size. Declines in fisheries production and catches have been documented in other parts of the world after implementation of flood control and drainage projects (e.g., Bangladesh: Sultana and Thompson 1997; Halls et al. 1998, 1999), but not in Australia (Cappo et al. 1998).

When artificial drainage occurs in coastal floodplains that contain acid sulfate soils, the impacts on aquatic habitats can be more severe. Acid sulfate soils are oxidized or unoxidized sulfidic sediments, which occur in coastal floodplains around the world (Dent 1986), including northern and eastern Australia (National Working Party on Acid Sulfate Soils 2000). Drainage of acid sulfate soils results in a buildup of sulfuric acid, iron, and aluminum in the sediment (White et al. 1997). Acute discharges of these chemicals into waterways following rain events can have immediate and severe impacts on water quality, such as acidification, high concentrations of dissolved aluminium, aluminium flocculation, iron precipitation, and lack of dissolved oxygen resulting from iron oxidation (Johnston et al. 2003 and references therein). Such reduction in water quality can result in epizootic ulcerative syndrome in fish (Callinan et al. 1996) and extensive fish and invertebrate kills (Callinan et al. 1996; Johnston et al. 2003; Walsh et al. 2004). Chronic acid sulfate discharge may create barriers to movement, potentially affecting the migration of fish and invertebrate species (Kroon 2005).

In this study, we examined the potential role of tidal floodgates in depleting estuarine and coastal fisheries stocks in coastal floodplains of eastern Australia. This study is part of a larger project that developed management options for gated drainage systems to improve water quality and fish passage in coastal catchments with acid sulfate soils. If tidal floodgates do deplete coastal fisheries stock, we predict the following. First, species assemblage structures of juvenile fishes and invertebrates will differ between reference and gated drainage systems. Second, juvenile fishes and invertebrates of species that migrate as part of their life cycle will be present at lower proportions in gated drainage systems. Third, environmental conditions in gated drainage systems will not be conducive to the maintenance of juveniles of economically important species. To test these predictions, we (*i*) observed and compared species community structures in reference and gated drainage systems and (*ii*) determined which environmental variables were associated with the observed patterns in species assemblages in the Clarence River estuary (New South Wales (NSW), Australia) over a 1-year period.

Materials and methods

Study area

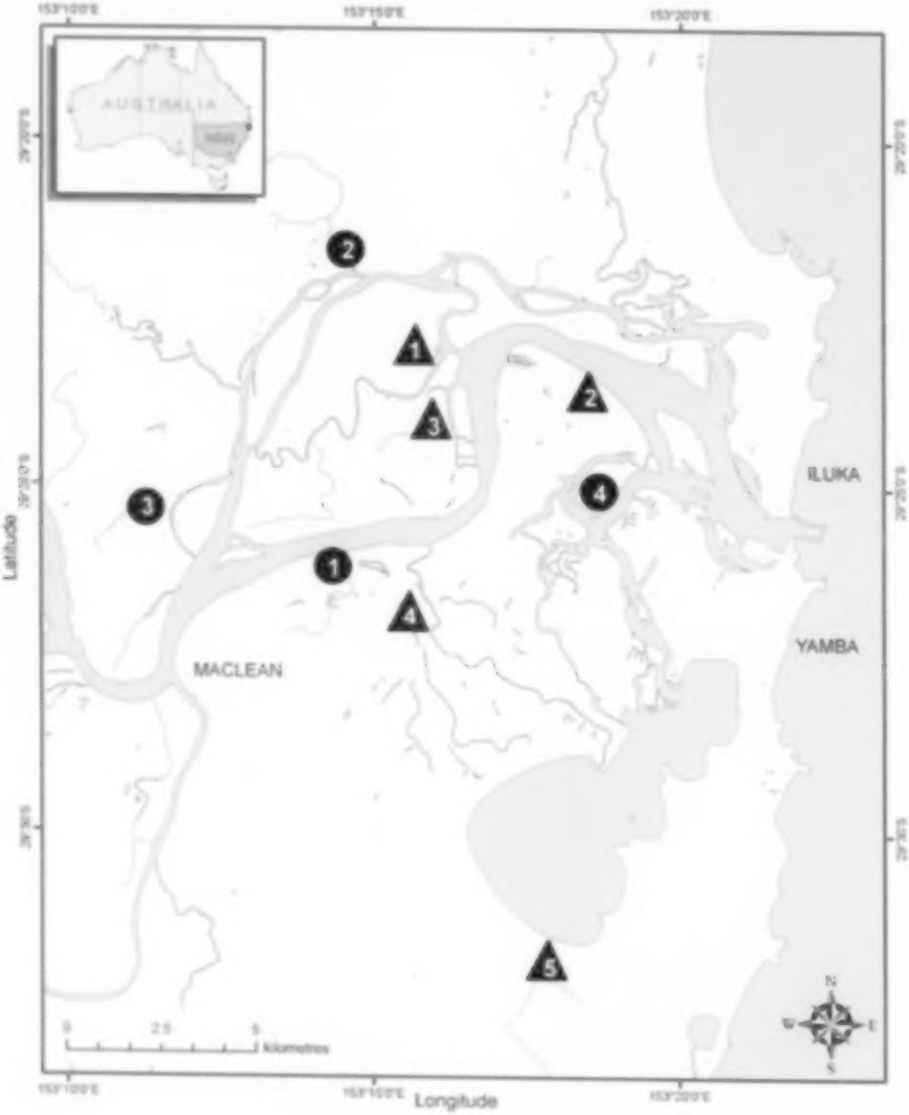
Our study was conducted in the Clarence River floodplain between Grafton and Yamba in northern NSW, Australia (Fig. 1). The Clarence River is NSW's largest coastal river system, with a catchment area of ~22 400 km^2 (Roy et al. 2001). The river's floodplain covers an area of 2100 km^2 (Bell and Edwards 1980) and is underlain by ~53 000 ha of acid sulfate soils (Tulau 1999). Extensive flood mitigation schemes have been constructed in the floodplain (Bell and Edwards 1980), including at least 1700 km of floodgated drainage systems and watercourses (Williams 2000). Almost all freshwater wetlands on the floodplain (14.7 km^2) are affected by grazing and drainage activities, and 84% of the total seagrass area (5.28 km^2) was lost between 1942 and 1986 (West 1992). Agricultural activities on the floodplain mainly comprise cultivation (sugarcane) and grazing (Williams 2000).

The lower reaches of the floodplain are extensively used for commercial and recreational fishing (Bell and Edwards 1980). Northern NSW, and in particular the Clarence River, has been supporting one of the largest estuarine commercial fisheries in NSW (Pease and Grinberg 1995). In 1999–2000, the Clarence River supported the largest number of commercial fishers (±20%) as well as the largest catch (~25% by weight and by value) in NSW's estuarine commercial fisheries (Tanner and Liggins 2001). The estuarine prawn fishery was valued at A$2.3 million, comprising ~75% of the value of the state's total estuary prawn fisheries catch (Montgomery and Craig 2001). The recreational harvest in the Clarence River is estimated to be similar to or higher than the commercial harvest, at least for the more popular fish species (West and Gordon 1994).

Study drainage systems

We consider nine drainage systems: four tributary streams without floodgates (reference drainage systems) and five flood mitigation channels with floodgates (gated drainage systems)

Fig. 1. Map of the Clarence River floodplain, northern New South Wales, Australia, with the nine drainage systems. ●, reference drainage systems (1, James Creek; 2, Mororo Creek; 3, Sandy Creek; 4, Thorny Creek); ▲, gated drainage systems (1, Carrols Drain; 2, Carrs Drain; 3, Harwoods Drain; 4, Marsh Drain; 5, Taloumbi #5).



(Fig. 1). The floodgates comprise one-way (downstream opening) flap valves, allowing water to drain out but restricting saltwater inflow and tidal exchange. Sampling sites were selected on the basis of the site location in the floodplain and landholders' permission to access their property. Spatially, the reference drainage systems encompassed the locations of the gated drainage systems in the floodplain. Given this distribution of sampling sites, we assumed similar species compositions at reference and gated systems. All systems have a high acid sulfate soil potential, with depth of the pyritic level ranging from 0–1 to 1–3 m, as determined from acid sulfate soil risk maps held by the NSW Department of Infrastructure, Planning and Natural Resources. The following site descriptions are drawn from Pollard and Hannan (1994), Williams (2000), the Clarence River County Council (J. Challacombe, Floodplain Project Manager, Clarence River County Council, Grafton NSW 2460, Australia, personal communication), and from personal observations.

Reference drainage systems

James Creek enters the Clarence River from the south, 5 km northeast of Maclean and 18 km from the mouth of the river. Near the mouth, the fringing vegetation consists of mangroves, while further upstream these are replaced by casuarinas, eucalypts, acacias, and lantana. The creek drains a catchment consisting of sugarcane near the mouth and primarily melaleuca backswamp used for cattle grazing further upstream. Part of the upstream catchment is a SEPP 14 wetland (referring to NSW State Environmental Planning Policy No. 14 – Coastal Wetlands, which applies to developments involving work that could damage or destroy wetlands).

Mororo Creek enters the Back Channel from the north, near its junction with the Clarence River's North Arm, 0.5 km west from Mororo bridge and 7.4 km from the river's mouth. Near the mouth the fringing mangroves are backed by sparse casuarinas, and the surrounding land use is sugarcane. Further upstream, land use consists of sugarcane, cattle grazing, and state forest. The creek drains a large melaleuca backswamp.

Sandy Creek enters Ashby Channel from the west, 3.5 km downstream from and to the north of Maclean, 1.5–2 km from the North Channel, and ~23 km from the mouth of the Clarence River. Near the mouth, the fringing vegetation of the creek consists mainly of mangroves, casuarinas, and eucalypts, with cattle grazing the surrounding land use.

Thorny Creek is located on Thorny Island, 5 km northwest of Yamba, and enters Romiaka Channel about 7 km from the river's mouth. The creek drains a dense mangrove forest on the south side of the island. Most of Thorny Island is SEPP 14 wetland. Thorny Island is a crown reserve and as such is relatively undisturbed.

Gated drainage systems

Carrolls Drain is situated on Chatsworth Island, 13 km from the mouth of the Clarence River. The mouth of the original creek has been blocked, and a new opening was constructed and gated (size of floodgates: 1.5 m × 1.5 m, with five box culverts) further to the south in 1966. Carrolls Drain is ~3 km long and connects with four private drains, adding another 2 km of drain. The surrounding land use is sugarcane, but 20% of the original 0.5 km^2 of wetland remains.

Carrs Drain is situated on Palmers Island, 8 km from the mouth of the Clarence River. The drain was constructed and floodgates (1.5 m × 1.5 m, with three box culverts) were installed in 1965. The 1.5 km channel upstream of the floodgates joins with three private drains, adding another 1 km of drain. The surrounding land use is pasture grass and sugarcane, but 50% of the original 2 km^2 wetland remains.

Harwoods Drain is situated on Harwood Island, 13 km from the mouth of the Clarence River. The drain was constructed and floodgates (1.5 m × 1.5 m, with three box culverts) were installed in 1966. The 2.5 km channel upstream of the floodgates does not join with any other drains. The surrounding land use is sugarcane, and none of the previous 0.2 km^2 wetland remains.

Marsh Drain is situated in the Palmers Channel area, 20 km from the mouth of the Clarence River. The drain was constructed and floodgates (1.5 m × 1.5 m, with two pipes) were installed in 1965. The pipe culverts are situated ~40 cm above a concrete apron. Marsh Drain is ~2 km long and joins with one private drain, adding another 2 km of drain. The surrounding land use is sugarcane, and none of the previous 1.5 km^2 wetland remains.

Taloumbi #5 is situated on the southside of Lake Wooloweyah, 23.9 km from the mouth of the Clarence River. The drain was constructed and floodgates (1.5 m × 1.5 m, with three pipe culverts) were installed in 1973. The 2.5 km channel upstream of the floodgates joins with three private drains, adding another 4 km of drain. The surrounding land use is pasture grass and sugarcane, and none of the previously substantial wetland remains.

Sampling methods

Quantitative samples were collected at all nine drainage systems every 2 months (September 2000 to July 2001), totalling six sampling occasions. Owing to two major floods in the Clarence River in February and March 2001, our scheduled trip in March was postponed until April. Since the samples were well separated in time, the samples collected within each drainage system were considered to be temporally independent. At each sampling site, two areas were selected for sampling: one area 40 m upstream (Area 1) from the mouth (i.e., barrier at gated sites) of the system and a second area (Area 2) 120 m upstream from the mouth (i.e., barrier at gated sites). Sites were sampled in a random order on each sampling occasion, and moon phase was not taken into consideration. In general, James Creek, Sandy Creek, and Thorny Island were sampled around high slack tide and Mororo Creek around low slack tide. While tidal changes in fish assemblages have been recorded (e.g., Morrison et al. 2002), habitat effects on species assemblages generally tend to override any tidal effects (e.g., Ribeiro et al. 2006). Consequently, we expected that the impact of tidal floodgates on species assemblages and environmental variables would override any potential differences due to sampling at different times of the tide.

Water quality

To minimize disturbance of the water column, bottom sediments, and aquatic fauna, water quality measurements and samples were taken while floating on a large rubber tube along a transect. During each sampling occasion, four water quality variables were measured and three water samples collected at each sampling area before the fish sampling commenced. At three equidistant points along a transect across the stream channel, we measured temperature (T, °C), salinity ($g \cdot L^{-1}$), pH, and dissolved oxygen (DO, $mg \cdot L^{-1}$), both at the surface and the bottom, using a TPS model 90FL or Horiba U-10 water quality meter. At the middle point, three water samples were collected, stored on ice, and frozen at the end of the day for the determination of conductivity (EC) ($dS \cdot m^{-1}$); total dissolved solids ($mg \cdot L^{-1}$); turbidity (nephelometric turbidity units, NTU); total phosphorus and phosphate ($mg \cdot L^{-1}$ P); total nitrogen, nitrate, nitrite, and ammonia ($mg \cdot L^{-1}$ N); total aluminum and dissolved aluminum ($mg \cdot L^{-1}$); and total iron and dissolved iron ($mg \cdot L^{-1}$). Water samples were analysed at the Environmental Analysis Laboratory (Certified Laboratory Practice, Reg. No. CLP0052), Centre for Coastal Management at Southern Cross University (Lismore, NSW, Australia). Water samples were collected, stored, and analysed according to the protocols in the American Public Health Association (1995).

Because of technical problems with the TPS water quality meter, DO could only be measured in November 2000 and April, May, and July 2001, and pH was not measured in January 2001. The January water samples were analysed for pH at the Environmental Analysis Laboratory. Turbidity was only measured in April, May, and July 2001.

Fishes and invertebrates

Juvenile fishes and invertebrates were sampled using a fine mesh seine net (10 m headline × 2 m drop × 6 mm stretch mesh). The net was set from the shore during daylight hours in a U shape, covering an approximate area of 50 m^2, then pursed up onto the shore. Species area curves for pilot samples in the Clarence River revealed that three seine hauls caught 86% of species present (Kroon et al. 2004). The design had three replicate samples at each of the sampling areas, yielding six seine hauls at each site on each sampling occasion. The replicates were positioned to avoid overlapping at any point.

Large fish (>150 mm standard length (SL, from the tip of the snout to the caudal peduncle)) were identified to species, measured (SL), weighed (g), checked for signs of advanced reproductive ripeness (exuding eggs or sperm), red spot disease, and overall condition, and then released alive. All remaining animals were first euthanased with ethyl *p*-amino-benzoate (benzocaine, 100 $mg{\cdot}L^{-1}$), then preserved in 10% formalin–seawater (Barker 1999) before being transported to the laboratory for processing.

Wherever possible, all fish and invertebrates in each seine haul were identified to species level with the aid of published keys (for references, see Kroon et al. 2004), and the total number of individuals per species was recorded. A few individuals of each species were sent to the Australian Museum (Sydney) to confirm their identification. After positive identification, species were assigned to be of economic importance for fisheries if described as an Australian seafood species in Yearsly et al. (1999). For each of these economically important species (Table 1), we measured the length of all individuals (results not presented here). For the remaining species, only the length of the smallest and the largest individuals was recorded. We measured SL for fish, carapace length for prawns (CL, 0.1 mm), and CL and carapace width (CW, 0.1 mm) for crabs. For each species, we measured total weight of all individuals combined. Finally, condition of individuals was noted, in particular the presence of epizootic ulcerative syndrome (Callinan et al. 1996). Subsamples from all trips were subsequently deposited with the relevant collection managers at the Australian Museum.

While we tried to avoid damaging specimens when sampling, many prawn and shrimp did sustain some damage. If we could not identify these specimens (or parts thereof) to species, they were not counted as individuals and not included in the abundance analyses. They were, however, combined and weighed as prawn bodies and shrimp bodies and subsequently included in the biomass analyses.

Habitat characteristics

Stream width (m) at water level was measured using the transect described above, and water depth (cm) was measured at the three equidistant points along this transect. The proportional contribution of each substratum type (mud (particle size <1 mm), sand (1–16 mm), fine gravel (17–32 mm), gravel (33–64 mm), cobbles (65–128 mm), boulders (>129 mm), and bedrock) was quantified by ranking on a 5-point scale, corresponding to absent (0), uncommon (1), common (2), abundant (3), and very abundant (4). The proportional contribution of each cover element (leaf litter, submerged vegetation (e.g., seagrass, other submerged vegetation), emergent vegetation (e.g., water lillies, grass and rushes), overhanging vegetation (mangroves, overhanging terrestrial trees), filamentous algae, large woody debris (Ø > 20 cm), small woody debris (Ø < 20 cm), undercut bank, and exposed rootmasses) were quantified by ranking on the same scale. Riparian cover (the proportional amount of stream surface area directly covered by riparian vegetation overhead, for the stretch of stream sampled for biota) was estimated by eye and placed into one of five riparian cover categories (1 = 0%–20%, 2 = 21%–40%, 3 = 41%–60%, 4 = 61%–80%, and 5 = 81%–100%). Surrounding land use (cattle grazing or sugarcane) was noted as absent (0) or present (1).

Data analyses

Life cycle categories in reference and gated drainage systems

To determine whether floodgates affect the abundance and biomass of specific life cycle categories in gated drainage systems, we compared the proportional contributions of these categories between reference and gated drainage systems for all six sampling occasions combined. If floodgates had no effect, we predicted that the proportional contributions of life cycle categories would not differ between reference (expected proportions) and gated (observed proportions) drainage systems.

Individual species were allocated to a life cycle category, modified from Young et al. (1997), based on their life history traits and ecological characteristics with the aid of published keys (for references, see Kroon et al. 2004; also Xiao and Greenwood 1993; Pusey et al. 2004 and references therein). Specific attention was given to the potential requirement of individual species for migration as part of their life cycle. Marine stragglers are marine species that enter estuaries only occasionally, in low numbers, and are usually found in the lower reaches. Marine estuarine opportunists are species that spawn in ocean but enter estuaries regularly, often in large numbers, and usually as juveniles. Estuarine–marine species are those that spend most of their lives in the estuary or coastal ocean waters; they generally spawn in the ocean and may enter freshwater from time to time. Estuarine species complete their life cycle in estuaries. Freshwater–estuarine species can complete the whole of their life cycle in either freshwater or estuarine environments. Catadromous species feed mainly in freshwater and to a lesser extent in the estuary but spawn in the ocean. Freshwater species are those whose life cycle is typically confined to fresh water. Taxa that could not be identified to species level (Table 1) or species for which not enough information was available were not categorized. The proportional contribution to each life cycle category was calculated for number of species, number of individuals, and biomass for all systems combined and for reference and gated systems separately. Subsequently, we compared the expected (reference systems) and observed (gated systems) frequencies of the life cycle categories in these three groupings using χ^2 tests.

Relationship between species assemblages and environmental variables

We compared species assemblages of both abundance and biomass between reference and gated systems for each sam-

Table 1. Total number (Total N), total weight (Total W), and life cycle categories of fish and invertebrate taxa captured in reference and gated drainage systems in the Clarence River floodplain from September 2000 to July 2001.

Species		Reference system		Gated system		
Scientific name	Common name	Total N	Total W	Total N	Total W	Life cycle[†]
Fishes						
*Anguilla reinhardtii**	Longfin eel	0	0	1	32	C
Atherinosoma microstoma	Smallmouth hardyhead	2	0	0	0	E
Melanotaenia duboulayi	Duboulay's rainbowfish	0	0	4	0	F
Gambusia holbrooki	Eastern Gambusia	157	34	11 442	1 704	F–E
Pseudomugil signifer	Pacific blue-eye	785	131	589	140	F–E
*Arrhamphus sclerolepis**	Snubnose garfish	36	313	0	0	F–E
Herklotsichthys castelnaui	Southern herring	8	196	0	0	E–M
*Hyperlophus vittatus**	Sandy sprat	63	16	0	0	E–M
*Engraulis australis**	Australian anchovy	1	1	0	0	E–M
Siphamia roseigaster	Pinkbreast siphonfish	15	11	0	0	S
Omobranchus anolius	Oyster blenny	1	1	0	0	E
Caranx spp.*	Unidentified *Caranx*	1	3	0	0	O
Ambassis agassizii	Agassiz's glassfish	357	83	61	21	F
Ambassis jacksoniensis	Port Jackson glassfish	2 795	1 819	33	23	E
Ambassis marianus	Estuary glassfish	2 121	8 132	31	58	E
Ambassis spp.	Unidentified *Ambassis*	227	20	345	17	—
Carassius auratus	Goldfish	0	0	12	1	F
*Gerres subfasciatus**	Common silver belly	139	544	36	13	E
*Girella tricuspidata**	Luderick	17	3	0	0	E–M
Microcanthus strigatus	Stripey	2	0	0	0	S
Afurcagobius tamarensis	Tamar goby	763	168	49	29	F–E
Arenigobius bifrenatus	Bridled goby	33	23	18	38	F–E
Arenigobius frenatus	Half-bridled goby	8	9	0	0	E
Arenigobius spp.	Unidentified *Arenigobius*	1	4	0	0	E
Butis butis	Crimsontip gudgeon	1	8	0	0	E
Cryptocentroides gobioides	Crested oystergoby	5	17	0	0	—
Favonigobius exquisites	Exquisite sand-goby	83	31	16	2	E
Gobiomorphus australis	Striped gudgeon	940	201	2 407	618	F
Gobiopterus semivestitus	Glassgoby	928	98	646	83	F–E
Hypseleotris compressa	Empire gudgeon	6 711	1 299	19 411	6 183	F
Hypseleotris galii	Firetaile gudgeon	26	4	245	28	F
Mugilogobius platynotus	Flatback mangrove goby	3	0	29	5	E
Pandaka lidwilli	Lidwill's dwarf goby	18	1	16	2	—
Philypnodon grandiceps	Flathead gudgeon	601	304	9 011	3 664	F
Philypnodon sp. 1	Dwarf flathead gudgeon	18	4	1 968	294	F
Pseudogobius sp. 9	A goby	2 482	389	2 218	670	E
Redigobius macrostomus	Large-mouth goby	395	88	38	14	F–E
Taenioides purpurascens	Purple eelgoby	1	1	1	3	E
Gobiidae spp.	Unidentified Gobiidae	12	0	251	2	—
Monodactylus argenteus	Diamondfish	27	47	1	0	E
*Liza argentea**	Flat-tail mullet	2 152	4 777	1	0	E–M
*Mugil cephalus**	Sea mullet	287	679	9	247	E–M
*Pomatomus saltatrix**	Tailor	3	13	0	0	O
*Scatophagus argus**	Spotted scat	1	3	0	0	E
*Selenotoca multifasciata**	Striped scat	2	3	0	0	E
*Acanthopagrus australis**	Yellowfin bream	518	458	13	581	E–M
*Rhabdosargus sarba**	Tarwhine	77	19	1	0	O
*Synaptura nigra**	Black sole	1	10	0	0	E
*Platycephalus fuscus**	Dusky flathead	4	595	0	0	E–M

Table 1 *(continued)*.

Species		Reference system		Gated system		
Scientific name	Common name	Total *N*	Total *W*	Total *N*	Total *W*	Life cycle[†]
Centropogon australis	Fortescue	14	144	0	0	E–M
Notesthes robusta	Bullrout	2	165	0	0	F–E
Tetractenos glaber	Smooth toadfish	6	356	0	0	E
Tetractenos hamiltoni	Common toadfish	1	12	0	0	E
Total		22 851	21 234	48 903	14 470	
Invertebrates						
Tetragnathidae spp.	Spider species	1	0	0	0	—
Conchostraca spp.	Clam shrimp species	0	0	23	2	—
Copepoda spp.	Copepod species	0	0	18	0	—
Amphipoda spp.	Amphipod species	0	0	9	0	—
Melita plumulosa	An amphipod species	0	0	125	1	F–E
Alpheus spp.	Snapping shrimp species	6	2	0	0	—
Caridina indistincta	A freshwater shrimp	7	1	35	2	F
Caridina nilotica	A freshwater shrimp	106	5	42	2	F
Paratya australiensis	Australian paratya	1	0	0	0	F
Australoplax tridentata	Furry-clawed crab	0	0	1	0	E
Paragrapsus laevis	Spotted smooth shore crab	1	1	0	0	E
Parasesarma erythodactyla	Red-fingered marsh crab	7	1	0	0	E
Sesarma erythrodactyla	An estuarine crab	0	0	1	0	E
Amarinus spp.	Spider crab species	45	4	126	26	—
Macrobrachium cf. *novaehollandiae*	New Holland river prawn	214	126	128	162	E
Palaemon debilis	A carid shrimp	6 608	768	4 509	446	F–E
Palaemonidae	Shrimp bodies	—	0	—	1	—
Metapenaeus bennettae[*]	Greentail prawn	2	5	6	1	E–M
Metapenaeus macleayi[*]	School prawn	6 834	2 398	546	460	E–M
Penaeus plebejus[*]	Eastern king prawn	185	15	58	91	E–M
Penaeidae	Prawn bodies	—	12	—	1	—
Thalamita crenata	Notched *Thalamita*	1	2	0	0	E
Acetes sibogae australis	Australian paste shrimp	258 947	13 656	12 773	644	E
Catoessa ambassae	An isopod	15	0	0	0	E
Cymodetta spp.	Pill bug species	16	0	195	3	—
Mysidacea spp.	Opposum shrimp species	2	0	23	1	—
Xenostrobus securis	A muscle	2	0	67	12	E
Corbicula australis	Australian corbicula	0	0	207	2	F
Spisula trigonella	Little trough shell	0	0	1	0	E
Fluviolanatus subtortus	A bivalve	7	1	640	68	E
Idiosepius spp.	Pygmy squid species	10	1	0	0	—
Tesseropora rosea	A barnacle	1	2	3	0	S
Bembicium auratum	Gold-mouthed conniwink	2	0	0	0	E
Nassarius burchardi	Burchard's dog whelk	2	0	2	0	E
Nassarius jonassii	Jona's dog whelk	5	0	2	1	E
Salinator fragilis	Fragile air-breather	1	0	52	4	E
Glyptophysa gibbosa	Alice's pouch snail	1	0	1	0	F
Melanoides spp.	Screwshell species	0	0	475	90	F
Ceratonereis aequisetis	A polychaete worm	0	0	104	13	E
Tipulidae spp.	Larvae of crane fly species	0	0	4	0	F
Diplonychus spp.	Giant water bug species	5	1	17	3	F
Corixidae spp.	Waterboatmen species	4	0	129	4	F
Naucoris spp.	Creeping water bug species	0	0	1	0	F
Notonectidae spp.	Backswimmer species	0	0	33	1	F
Anisoptera spp.	Larvae of dragonfly species	2	0	32	5	F

Table 1 (*concluded*).

Species		Reference system		Gated system		
Scientific name	Common name	Total *N*	Total *W*	Total *N*	Total *W*	Life cycle[†]
Zygoptera spp.	Larvae of damselfy species	0	0	54	2	F
Total		273 040	17 004	20 442	2 047	

Note: 10 individual fish (each >500 g) with a combined weight of more than 12 kg were excluded from the analysis and were not included in the table. Species are given in taxonomic order; an asterisk (*) indicates species of economic importance; a dash (—) indicates a taxon was not allocated to a life cycle category.

[†] S, marine straggler; O, marine estuarine opportunist; E–M, estuarine–marine; E, estuarine; F–E, freshwater–estuarine; C, catadromous; F, freshwater.

pling occasion using nonmetric multivariate data analysis techniques (Primer 5.0 package, Plymouth Marine Laboratory, UK). These techniques are based on measures of similarity that indicate the degree that species are shared among samples (Clarke and Warwick 2001). We averaged the number of individuals (or biomass) per species across the three seine shot replicates made within a sampling area, resulting in two replicates within a sampling site for each sampling occasion.

To graphically represent relationships amongst assemblages, we used the Bray–Curtis similarity coefficient to calculate similarity matrices between reference and gated systems (Clarke and Warwick 2001). Data were standardized and $\log(x + 1)$-transformed, and similarity matrices were subsequently plotted using nonmetric multidimensional scaling (nMDS) ordinations (Clarke 1993; Manly 1994). We measured the goodness of fit between the configuration distances and the disparities, or the adequacy of the nMDS technique, by "stress" (Manly 1994). Stress values less than 0.1 indicate that the ordination is a good representation of the data. Stress levels greater than 0.2 indicate that the results should be treated with caution in interpreting any apparent pattern in the samples (Clarke and Warwick 2001).

To determine which species contributed to the highest levels of dissimilarity between reference and gated systems, we used the SIMPER (similarity of percentages) procedure (Clarke and Warwick 2001). Data were standardized and $\log(x + 1)$-transformed, and species were subsequently listed in decreasing order of their importance in discriminating between different groups of samples (Clarke and Gorley 2001).

To determine whether the composition of the species assemblages differed significantly between reference and gated systems, nested ANOSIM (analysis of similarity) tests were performed on similarity matrices. The ANOSIM procedure is based on the *R* statistic, which is compared with a distribution of *R* statistics (based on the null hypothesis of no differences). If the calculated value of *R* looks unlikely to have come from this distribution (depending on the level of significance, i.e., 5%), there is evidence to reject the null hypothesis (Clarke and Warwick 2001).

Finally, to examine which environmental variables were associated with the observed patterns in species assemblages between reference and gated systems, we used the BIOENV procedure. This calculates a harmonic rank correlation coefficient based on the similarity matrices of both the biotic and abiotic data (Clarke and Ainsworth 1993; Clarke and Warwick 2001). The larger the coefficient for a particular abiotic variable (or set of variables), the better the environmental variables are in explaining the biotic data (Clarke and Ainsworth 1993; Clarke and Warwick 2001). To determine which combination of environmental variables best explained the nMDS patterns, water and habitat quality data, as well as the presence or absence of a floodgate at a drainage system, were included simultaneously in BIOENV; environmental data were standardized and $\log(x + 1)$-transformed. Concentrations of nutrients, iron, and aluminium below detection levels were entered into the BIOENV analysis at half the detection level. Rather than using Euclidean distances to calculate similarity matrices (Clarke and Ainsworth 1993), we used the Bray–Curtis similarity coefficient because the environmental variables' matrices were dominated by zero counts. For each nMDS pattern, the best one- to five-variable combinations were determined, and correlation coefficients were plotted against the number of variables. The number of variables, after which adding extra variables did not contribute significantly to the correlation coefficient, was taken as the combination that best explained the nMDS patterns.

Results

General

Identification of taxa

Small juveniles of some fish and invertebrate species and adults of some invertebrate species proved difficult to identify. Small juveniles of certain fish and invertebrate species could not be identified to species level (e.g., *Ambassis* species and *Amarinus* species) and were therefore only identified to the genus level (e.g., as *Ambassis* spp., *Amarinus* spp.). Species of the pistol shrimp family Alpheidae are difficult to tell apart (S. de Grave, Assistant Curator of Zoology, Oxford University Museum of Natural History, Oxford, UK, personal communication). While both the Australian Museum and Oxford University Museum of Natural History identified two species in our samples (*Alpheus richardsoni* Yaldwyn, 1971 and *Alpheus* sp.), we combined all Alpheidae species into *Alpheus* spp. We found two species (*Macrobrachium* cf. *novaehollandiae* and *Macrobrachium intermedium*) of the shrimp family Palaemonidae difficult to separate. Three adult males were identified as *Macrobrachium* cf. *novaehollandiae* de Man, 1908 (S. de Grave, personal communication). Juvenile and female *Macrobrachium* spp., including those we identified as *M. intermedium*, were also considered by S. de Grave to be *Macrobrachium* cf. *novaehollandiae* based on rostral similarities. Hence, all *Macrobrachium* samples were recorded as *Macrobrachium* cf. *novaehollandiae*. The introduced screw-shell species *Melanoides tuberculata* Müller, 1774 and the endemic species *Melanoides ultra* Iredale, 1943 (previously *Stenomelania denisoniensis ultra* Iredale, 1943) do not exhibit a simple, obvious external character at the 1–3 cm size range to tell them apart (I. Loch, Malacology Collection

Supervisor, Australian Museum, 6 College Street, Sydney, NSW 2010, Australia, personal communication). To prevent misidentification, we labelled both screwshell species as *Melanoides* spp. Finally, species we initially identified as *Palaemon debilis* Dana, 1852 and *Palaemonetes atrinubes* Bray, 1976 were later combined into *Palaemon debilis*. Our samples are currently closest to *Palaemon debilis*, although they may prove to be a new species altogether (S. de Grave, personal communication).

Gear selectivity

Overall, the gear proved to be selective for small fish and invertebrates species and juveniles of larger species. Fishes and invertebrates of economic importance (Table 1) were collected in the size range from 5.3 to 950 mm SL and 0.4 to 24.5 mm CL, respectively. However, 96% of the fish were ≤80 mm SL, and 99.7% of the prawns were ≤20 mm CL. Because our study focussed on small species and juvenile fishes and invertebrates, 10 individual fish (each >500 g) with a combined weight of more than 12 kg were excluded from the analyses, including one yellowfin bream (*Acanthopagrus australis*), three longfin eels (*Anguilla reinhardtii*), two stingrays (*Dasyatis fluviorum*, *Dasyatis* spp.), one oxeye herring (*Megalops cyprinoides*), and three sea mullet (*Mugil cephalus*).

Total abundance and biomass of taxa and individuals

A total of 324 seines were hauled, yielding 97 taxa (53 fish and 44 invertebrate taxa), 365 236 individuals (71 754 fish and 293 482 invertebrates), and a combined weight of ~54.8 kg (35.7 kg fish and 19.1 kg invertebrates) (Table 1). Of these totals, 19 of the taxa (20%) were of economic importance (16 fish and 3 invertebrate species), accounting for 10 994 (3.0%) of the individuals (3363 fish and 7631 invertebrates) and ~11.3 kg (20.6%) of the weight (8.3 kg of fish and 3.0 kg of invertebrates) (Table 1). While the Australian paste shrimp *Acetes sibogae australis* Colefax, 1940 was by far the most common species, accounting for 74.4% of the total abundance and 26.1% of the total biomass, more than 60% was captured in 1 month (July 2001).

Species abundance and biomass in reference and gated drainage systems

Overall, more taxa were collected in reference systems (80 taxa: 50 fishes and 30 invertebrates) than in gated systems (65 taxa: 30 fishes and 35 invertebrates) (Table 1). Both overall abundance and biomass were higher in reference systems (295 891 individuals, 38.2 kg) than in gated systems (69 345 individuals, 16.5 kg). Reference systems also contained more economically important species (18 taxa: 15 fishes and 3 prawns) than did gated systems (9 taxa: 6 fishes and 3 prawns). Both abundance and biomass of economically important fish and prawn species were higher in reference systems (fishes: 3302 individuals, 7.4 kg; prawns: 7021 individuals, 2.4 kg) than in gated systems (fishes: 61 individuals, 0.9 kg; prawns: 610 individuals, 0.6 kg).

In reference systems, the Australian paste shrimp *Acetes sibogae australis* was by far the most common species, accounting for 87.5% of the total number of individuals and 35.7% of the total biomass. However, ~60% of these were captured in 1 month (July 2001). In contrast, in gated systems the empire gudgeon *Hypseleotris compressa* was the most common species (28% of individuals, 37.5% of biomass), followed by *Acetes sibogae australis* (18.4% of individuals, 3.9% of biomass), and the eastern Gambusia *Gambusia holbrooki* (16.5% of individuals, 10.3% of biomass).

Life cycle categories in reference and gated drainage systems

Thirteen taxa (4 fish and 9 invertebrate taxa) could not be categorized, resulting in some of the proportions not adding up to 100% in Table 2. Overall, the majority of the taxa were categorized as estuarine (34 species, 35.1%), followed by freshwater (21 species, 21.6%), and estuarine–marine (12 species, 12.4%) (Table 2). While this pattern was similar in both reference and gated systems, the proportional contribution to each life cycle category was significantly different for number of species ($\chi^2 = 19.85$, df = 6, $p < 0.003$). In particular, estuarine taxa made up a larger proportion in reference systems (37.5%) than in gated systems (29.2%), while freshwater taxa were more common in gated systems (30.8%) than in reference systems (16.3%).

The majority of individuals were categorized as estuarine (283 015 individuals, 77.5%), followed by freshwater (42 928 individuals, 11.8%), and freshwater–estuarine (27 123, 7.4%) (Table 2). The proportional contribution to each life cycle category in reference and gated systems was significantly different for number of individuals ($\chi^2 = 906.95$, df = 6, $p < 0.000\,000\,1$). In reference systems, the majority of individuals (90.2%) were categorized as estuarine, followed by estuarine–marine (3.4%). In contrast, in gated systems the majority of individuals (49.2%) were categorized as freshwater, followed by freshwater–estuarine (25.1%), and estuarine (23.3%).

Most of the biomass was categorized as estuarine (26.8 kg, 49.0%), followed by freshwater (12.8 kg, 23.4%), and estuarine–marine (10.7 kg, 19.5%) (Table 2). The proportional contribution to each life cycle category in reference and gated systems, however, was significantly different for biomass ($\chi^2 = 826.26$, df = 6, $p < 0.000\,000\,1$). In reference systems, most of the biomass (65.8%) was categorized as estuarine, followed by estuarine–marine (24.3%). In contrast, in gated systems most of the biomass (66.1%) was categorized as freshwater, followed by freshwater–estuarine (14.9), and estuarine (10.2%).

Relationship between species assemblages and environmental components

The ordinations showed clear separations between the reference and gated drainage systems for both the abundance and biomass assemblages across all six sampling occasions (Figs. 2*a*, 2*b*). Moreover, samples collected at a single site were generally located together within one sample occasion, indicating the similarity between these samples (Figs. 2*a*, 2*b*). All 12 ordinations were good representations of the data, with stress levels ranging from 0.08 to 0.13. This suggests that samples from the reference systems were consistently more similar to each other than to those from the gated systems and vice versa.

SIMPER revealed that the first 10 species that contributed to the total average dissimilarities in assemblages between reference and gated drainage systems explained 75.50% to 85.89% of this dissimilarity in abundance assemblages and 74.13% to 87.79% in biomass assemblages, respectively (Ta-

Table 2. Percent contribution (%) to each life cycle category in the Clarence River floodplain and in both reference and gated drainage systems of the floodplain for numbers (*N*) of species and indivuals and species biomass (*B*, in g) between September 2000 and July 2001.

Life cycle category	All systems		Reference systems		Gated systems	
	N or *B*	%	*N* or *B*	%	*N* or *B*	%
Species						
Marine straggler	3	3.1	3	3.8	1	1.5
Marine estuarine opportunist	3	3.1	3	3.8	1	1.5
Estuarine–marine	12	12.4	12	15.0	6	9.2
Estuarine	34	35.1	30	37.5	19	29.2
Catadromous	1	1.0	0	0.0	1	1.5
Freshwater–estuarine	10	10.3	9	11.3	8	12.3
Freshwater	21	21.6	13	16.3	20	30.8
Total	84	86.6	70	87.7	56	86
Individuals						
Marine straggler	21	<0.1	18	<0.1	3	<0.1
Marine estuarine opportunist	82	<0.1	81	<0.1	1	<0.1
Estuarine–marine	10 718	2.9	10 085	3.4	633	0.9
Estuarine	283 015	77.5	266 879	90.2	16 136	23.3
Catadromous	1	<0.1	0	0.0	1	<0.1
Freshwater–estuarine	27 123	7.4	9 707	3.3	17 416	25.1
Freshwater	42 928	11.8	8 779	3.0	34 149	49.2
Total	363 888	99.6	295 549	99.9	68 339	98.5
Biomass						
Marine straggler	13	<0.1	13	<0.1	0	0.0
Marine estuarine opportunist	35	0.1	35	0.1	0	0.0
Estuarine–marine	10 669	19.5	9 288	24.3	1 381	8.4
Estuarine	26 835	49.0	25 156	65.8	1 679	10.2
Catadromous	32	0.1	0	0.0	32	0.2
Freshwater–estuarine	4 242	7.7	1 788	4.7	2 454	14.9
Freshwater	12 819	23.4	1 901	5.0	10 918	66.1
Total	54 645	99.8	38 181	99.9	16 464	99.8

Note: Taxa that could not be identified to species level (Table 1) or species for which not enough information was available were not categorized (13 taxa in total). This resulted in some of the percentages not adding up to 100%.

ble 3). For the abundance assemblages, 16 species out of the 97 taxa collected were most important in contributing to the dissimilarities, with 5 of these 16 species (*Acetes sibogae australis*, *Hypseleotris compressa*, *Metapenaeus macleayi* (Haswell, 1879), *Phylipnodon grandiceps*, and the exotic *Gambusia holbrooki*) consistently contributing. *Gambusia holbrooki* was consistently more abundant in gated systems, while *Hypseleotris compressa* and *Phylipnodon grandiceps* were more abundant in gated systems on five out of the six sampling occasions. In contrast, *Acetes sibogae australis* and *Metapenaeus macleayi* were consistently more abundant in reference systems. For the biomass assemblages, 17 species out of the 97 taxa collected were most important in contributing to the dissimilarities, with three of these (*Hypseleotris compressa*, *Metapenaeus macleayi*, and *Phylipnodon grandiceps*) consistently contributing. Biomass of *Hypseleotris compressa* and *Phylipnodon grandiceps* was greater in gated systems on five out of the six sampling occasions. In contrast, biomass of *Metapenaeus macleayi* was consistently higher in reference systems. Six economically important species contributed to the total average dissimilarities, namely *Acanthopagrus australis*, *Arrhamphus sclerolepis*, *Gerres subfasciatus*, *Liza argentea*, *Metapenaeus macleayi*, and *Mugil cephalus*.

Nested ANOSIM revealed that in four out of six sampling occasions (September, November, January, and May), samples collected in reference systems were significantly different from those collected in gated systems (Table 4). In April and July, the treatment effect was nonsignificant.

BIOENV revealed that various combinations of 10 out of the 48 water and habitat quality variables best described the biotic patterns shown in the nMDS ordinations (Table 5; Figs. 2*a*, 2*b*, 3). The correlations between the combination of environmental variables and the biotic patterns shown in the nMDS ordinations (Figs. 2*a*, 2*b*) ranged from 0.579 to 0.810 for abundance ordinations and from 0.634 to 0.811 for biomass ordinations, respectively (Table 5). nMDS patterns of abiotic variables (Fig. 3) generally matched those of the biotic patterns (Figs. 2*a*, 2*b*); in May, an nMDS for abiotic variables could not be plotted because of the matrix being

Fig. 2. Nonmetric multidimensional scaling (nMDS) ordinations of species assemblages based on (*a*) abundance data and (*b*) biomass data on each of the six sampling occasions in the Clarence River floodplain in reference (○) and gated drainage systems (■). The ordinations are based on standardized, log(*x* + 1)-transformed abundances (or biomass) and Bray–Curtis similarities.

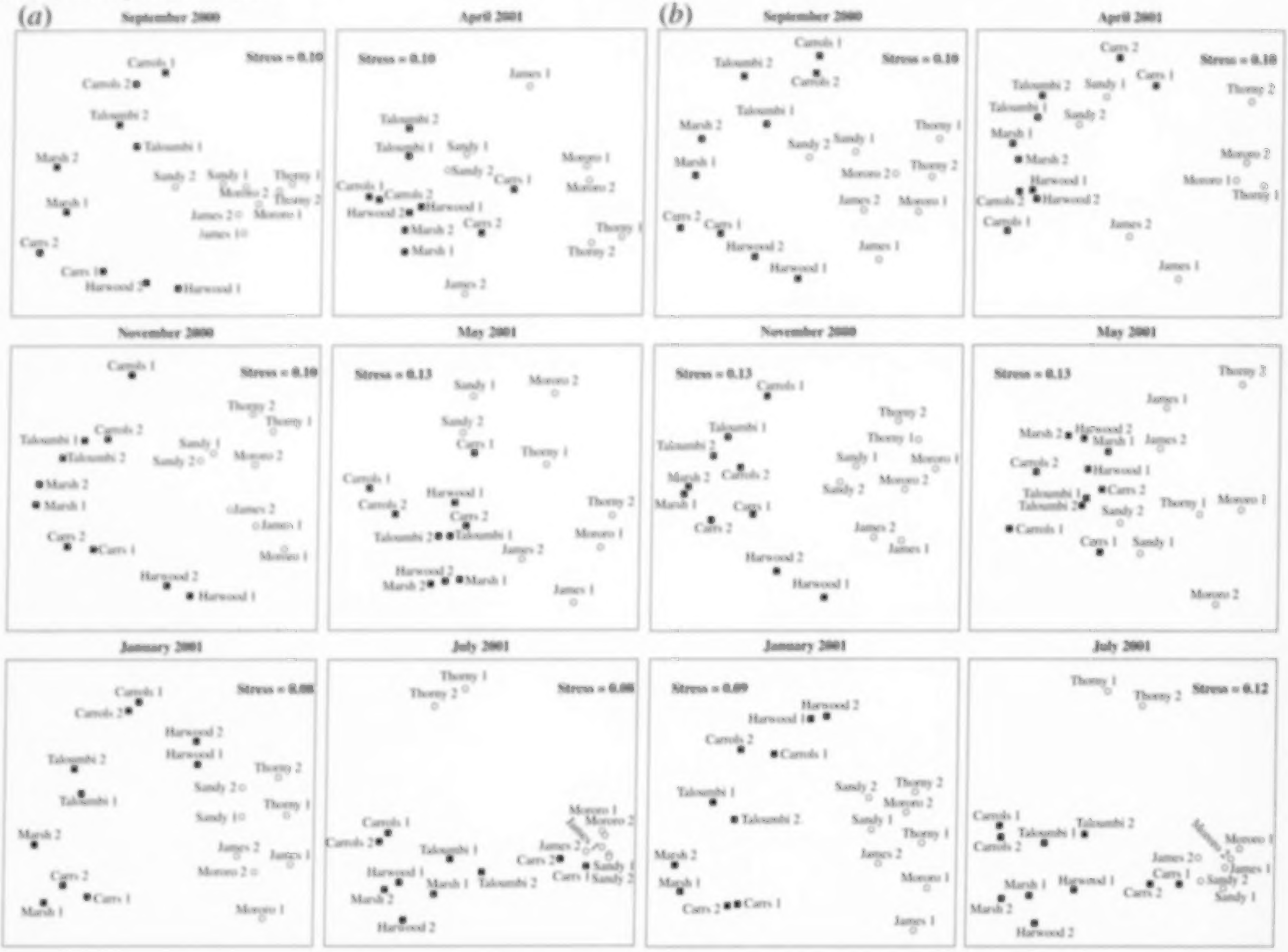


Table 3. SIMPER results showing the species ranked in decreasing order of importance (1–10 only) that contributed to the total average dissimilarity in species assemblages based on (*i*) abundance data and (*ii*) biomass data between treatments (reference vs. gated drainage systems) for the six sampling occasions in the lower Clarence River floodplain.

Species		2000		2001			
Scientific name	Common name	September	November	January	April	May	July
Abundance data							
*Acanthopagrus australis**	Yellowfin bream	**8**	—	—	—	—	—
Acetes sibogae australis	Australian paste shrimp	**3**	**2**	**10**	**10**	**1**	**1**
Afurcagobius tamarensis	Tamar goby	—	**10**	—	—	—	—
Ambassis jacksoniensis	Port Jackson glassfish	—	**6**	**9**	**2**	**9**	—
Ambassis marianus	Estuary glassfish	—	—	**8**	**7**	**7**	—
Gambusia holbrooki	Eastern Gambusia	9	8	3	1	3	4
Gobiomorphus australis	Striped gudgeon	—	—	—	9	4	3
Gobiopterus semivestitus	Glassgoby	—	—	—	—	10	**10**
Hypseleotris compressa	Empire gudgeon	2	1	1	3	**2**	2
*Liza argentea**	Flat-tail mullet	**7**	**9**	**2**	**6**	—	—
*Metapenaeus macleayi**	School prawn	**5**	**7**	**7**	**4**	**5**	**7**
Palaemon debilis	A carid shrimp	**1**	3	**4**	—	**8**	**6**
Philypnodon grandiceps	Flathead gudgeon	4	4	6	**5**	6	5
Philypnodon sp. 1	Dwarf flathead gudgeon	—	—	—	—	—	8
Pseudogobius sp. 9	A goby	**6**	**5**	**5**	—	—	9
Pseudomugil signifer	Pacific blue-eye	**10**	—	—	8	—	—
Average dissimilarity (%)[1]		80.01	85.89	82.82	77.35	76.70	75.50
Cumulative contribution (%)[2]		66.71	61.24	64.10	67.39	68.20	74.29
Biomass data							
*Acanthopagrus australis**	Yellowfin bream	8	—	**8**	—	—	—
Acetes sibogae australis	Australian paste shrimp	**4**	**10**	—	—	**4**	**1**
Ambassis jacksoniensis	Port Jackson glassfish	—	**6**	**9**	**4**	**9**	—
Ambassis marianus	Estuary glassfish	—	**9**	**3**	**7**	**3**	—
*Arrhamphus sclerolepis**	Snubnose garfish	—	—	—	**8**	—	—
Gambusia holbrooki	Eastern Gambusia	10	—	5	1	5	6
*Gerres subfasciatus**	Common silver belly	—	**5**	—	—	—	—
Gobiomorphus australis	Striped gudgeon	—	—	—	**9**	2	3
Hypseleotris compressa	Empire gudgeon	1	1	2	2	**1**	2
*Liza argentea**	Flat-tail mullet	**6**	**2**	**1**	**3**	**10**	—
*Metapenaeus macleayi**	School prawn	**3**	**3**	**10**	**5**	**6**	**5**
*Mugil cephalus**	Sea mullet	—	—	—	—	8	**10**
Palaemon debilis	A carid shrimp	**2**	7	**7**	—	—	**9**
Philypnodon grandiceps	Flathead gudgeon	5	4	4	**6**	7	4
Philypnodon sp. 1	Dwarf flathead gudgeon	—	—	—	—	—	8
Pseudogobius sp. 9	A goby	7	8	6	—	—	7
Pseudomugil signifer	Pacific blue-eye	**9**	—	—	10	—	—
Average dissimilarity (%)[1]		79.85	87.79	84.00	79.16	77.61	74.13
Cumulative contribution (%)[2]		59.59	59.60	62.19	70.25	67.81	72.71

Note: Numbers in bold indicate species that were more abundant in reference sites; an asterisk (*) indicates species of economic importance.

[1] Percentage of average dissimilarity between treatments for each sampling occasion.

[2] Percentage of cumulative contribution by first 10 species to dissimilarity.

dominated by zeros. For both abundance and biomass ordinations, BIOENV showed that floodgates and nutrients (total phosphorus, phosphate, total nitrogen, and nitrite) contributed to the combinations of environmental variables in five out of the six sampling occasions, with nutrient concentrations consistently higher in gated systems. Seagrass, other submerged vegetation, and grasses and rushes each contributed to the combinations of environmental variables once, with seagrass more abundant at reference systems and other submerged vegetation and grasses and rushes more abundant at gated systems. By-products of acid sulfate soil discharge, such as acidity (pH), total and dissolved aluminum, and total and dissolved iron, did not contribute to any of these combinations of environmental variables.

Table 4. Summary of two-way nested analysis of similarities (ANOSIM) tests examining differences among species assemblages, based on (*i*) abundance data and (*ii*) biomass data, between treatments (reference vs. gated drainage systems) for the six sampling occasions in the lower Clarence River floodplain.

Year	Month	Source of variation	Permutations	Global *R*	Significance level
Abundance data					
2000	September	Treatment	126	0.328	**3.2%**
		Location(Treatment)	999	0.907	**0.1%**
	November	Treatment	126	0.431	**2.4%**
		Location(Treatment)	999	0.726	**0.2%**
2001	January	Treatment	126	0.409	**3.2%**
		Location(Treatment)	999	0.904	**0.1%**
	April	Treatment	126	0.144	22.2%
		Location(Treatment)	999	0.820	**0.1%**
	May	Treatment	126	0.413	**1.6%**
		Location(Treatment)	999	0.593	**0.3%**
	July	Treatment	126	0.166	15.1%
		Location(Treatment)	999	0.808	**0.1%**
Biomass data					
2000	September	Treatment	126	0.356	**4.8%**
		Location(Treatment)	999	0.919	**0.1%**
	November	Treatment	126	0.513	**1.6%**
		Location(Treatment)	999	0.837	**0.1%**
2001	January	Treatment	126	0.469	**2.4%**
		Location(Treatment)	999	0.758	**0.1%**
	April	Treatment	126	0.231	10.3%
		Location(Treatment)	999	0.692	**0.1%**
	May	Treatment	126	0.325	**1.6%**
		Location(Treatment)	999	0.692	**0.1%**
	July	Treatment	126	0.200	12.7%
		Location(Treatment)	999	0.817	**0.1%**

Note: Significance levels in bold are $p < 0.05$.

Discussion

Our results show that species community structures in reference and gated drainage systems in the Clarence River floodplain are significantly different. First, the results support our prediction that species assemblage structures of juveniles (based on either abundance or biomass) differ significantly between reference and gated drainage systems, examined on four out of the six sampling occasions. Second, our result support our prediction that juvenile fishes and invertebrates of species that migrate as part of their life cycle are present at significantly lower proportions in gated drainage systems. This includes economically important species such as *Acanthopagrus australis*, *Arrhamphus sclerolepis*, *Gerres subfasciatus*, *Girella tricuspidata*, *Liza argentea*, *Metapenaeus macleayi*, *Mugil cephalus*, and *Rhabdosargus sarba*. These results are the first to document an impact of flood mitigation schemes on juvenile invertebrates and are in general agreement with similar studies on the impact of flood mitigation schemes on fish species assemblages (Pollard and Hannan 1994; Halls et al. 1998; Gibbs et al. 1999).

Our results indicate that closed floodgates act as physical barriers to juvenile fishes and invertebrates directly, but may also influence fish and invertebrate abundances indirectly by affecting environmental conditions within gated drainage systems. The presence in gated systems of juveniles of migratory fish and prawn species, such as *Acanthopagrus australis*, *Metapenaeus bennettae* Racek & Dall, 1965, *Metapenaeus macleayi*, *Mugil cephalus*, and *Penaeus plebejus* (Hess, 1865), demonstrates that floodgates do not provide a perfect seal. Individuals of these species may be small enough to move through cracks in floodgates during flood tides or strong enough to enter the gated systems against the flow during ebb tides. The relatively low numbers of these species in gated systems compared with reference systems, however, indicate that upstream movement of juvenile fishes and invertebrates is severely reduced by floodgates.

If juvenile fishes and invertebrates do succeed in moving upstream past floodgates, our BIOENV results indicate that specific combinations of reduced water quality and habitat condition may not be conducive to their survival in gated systems. We expected that by-products of acid sulfate soil discharge, such as acidity (pH), total and dissolved aluminum, and total and dissolved iron, would be a consistent component in the combination of environmental variables associated with the biotic nMDS patterns, because (*i*) all our study

Table 5. BIOENV results showing combinations of environmental variables that best describe the biotic patterns shown in the nonmetric multidimensional scaling (nMDS) ordinations of species assemblages based on (*i*) abundance data (Fig. 2*a*) and (*ii*) biomass data (Fig. 2*b*) for the six sampling occasions in the lower Clarence River floodplain.

	2000		2001			
Environmental variable	September	November	January	April	May	July
Abundance data						
Correlation coefficient	0.665	0.810	0.732	0.665	0.579	0.631
Conductivity (dS·m^{-1})			*			
Total phosphorus (mg·L^{-1} P)				*		
Phosphate (mg·L^{-1} P)			*			*
Total nitrogen (mg·L^{-1} N)	*	*				
Seagrass						**
Other submerged vegetation	*					
Grasses and rushes		*				
Cattle grazing					*	
Floodgates	*	*	*	*	*	
Biomass data						
Correlation coefficient	0.681	0.811	0.741	0.640	0.634	0.658
Conductivity (dS·m^{-1})			*			
Phosphate (mg·L^{-1} P)			*			*
Total nitrogen (mg·L^{-1} N)	*	*				
Nitrite (mg·L^{-1} N)				*		
Seagrass						**
Other submerged vegetation	*					
Grasses and rushes		*				
Cattle grazing					*	
Floodgates	*	*	*	*	*	

Note: Double asterisks (**) indicate that the environmental component was more common at reference drainage systems. The correlation coefficient (Spearman), based on the similarity matrices of both the biotic and abiotic data, is given for each sampling occasion.

sites have a high acid sulfate soil potential, (*ii*) concentrations of acid sulfate by-products were generally higher at our gated sites (F. Kroon, unpublished data), and (*iii*) floodgates result in a build-up of acid in gated drainage systems (White et al. 1997). In contrast, these by-products never contributed to any of these combinations. Given that fish diseases and fish kills have been directly related to acute acid sulfate discharges (Callinan et al. 1996; Johnston et al. 2003; Walsh et al. 2004), and chronic acid sulfate discharge may create barriers to fish and prawn movement (Kroon 2005), it is most likely that in our study, other environmental variables have overridden any potential effect of these by-products on patterns of species assemblages. Similarly, despite significantly higher proportions of freshwater taxa, individuals, and biomass in gated drainage systems, the combinations of environmental variables derived from the BIOENV procedure only twice included a variable directly related to salinity (conductivity). This suggests that while salinity may have affected abundance of individual species in gated systems, other environmental variables have a more substantial effect on species assemblages.

Our BIOENV results show that nutrient concentrations are a major component in explaining the observed nMDS patterns and are consistently higher in gated systems. Moreover, nutrient concentrations (total phosphorus, phosphate, and total nitrogen) in gated systems are significantly more often above Australian and New Zealand Environment and Conservation Council (ANZECC) trigger values (for lowland rivers and streams in southeast Australia; ANZECC 2000) than those in reference systems (Kroon et al. 2004). To our knowledge, this is the first documentation of a relationship in coastal floodplains between nutrient concentrations and species assemblages at a trophic level higher than primary production. The elevated levels of nutrients in gated systems are most likely related to (*i*) more intensive land use (Gabric and Bell 1993; Smith et al. 1999) surrounding these systems, (*ii*) the absence of a riparian zone trapping sediment and nutrients (Naiman and Décamps 1997), and (*iii*) retention of nutrients by floodgates (SPCC 1978). We speculate that higher nutrient concentrations in gated systems may affect species assemblages by influencing the structure of the aquatic food web, particularly through influencing species composition of primary producers (Gabric and Bell 1993). In gated systems, increased nutrient concentrations may have resulted in the disappearance and continued absence of seagrasses (e.g., Walker and McComb 1992; Short and Burdick 1996), as well as an increased production of aquatic weeds (grasses and rushes; other submerged vegetation) (SPCC 1978; Cappo et al. 1998).

Juveniles of most of the species of economic importance captured in the reference systems recruit into shallow man-

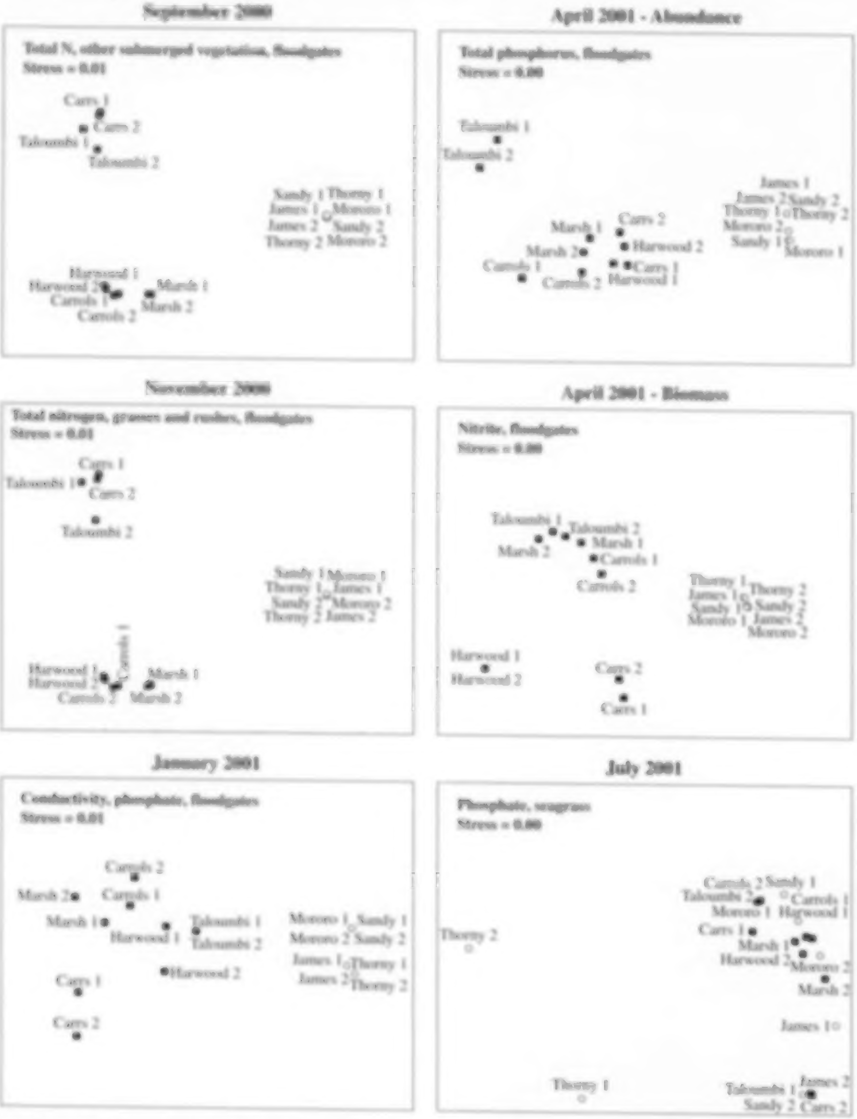


Fig. 3. Nonmetric multidimensional scaling (nMDS) ordinations of combinations of environmental variables on five of the six sampling occasions in the Clarence River floodplain in reference (○) and gated drainage systems (■). An nMDS for abiotic variables could not be plotted for May 2001 because of the matrix being dominated by zeros. The ordinations are based on standardized, $\log(x + 1)$-transformed environmental variables and Bray–Curtis similarities.

grove or seagrass habitats when first settling into coastal floodplains (SPCC 1981; Cappo et al. 1998; Hannan and Williams 1998). Both habitats provide a combination of shelter and food for juveniles of many fisheries species (Bell and Pollard 1989; Robertson and Blaber 1992), and the absence of these habitats in gated systems (Pollard and Hannan 1994; this study) could impact detrimentally on the settlement of potential recruits. In the Swartvlei estuary, a decline in abundance and condition of juvenile *Monodactylus falciformes* and *Rhadbosargus holubi* was associated with prolonged aquatic macrophyte senescence; this decline was mainly related to the collapse of invertebrate stock associated with the macrophytes (Whitfield 1984). Conversely, extensive growth of macroalgae in the Peel–Harvey estuary, as a result of nutrient enrichment, lead to an increase in fish abundance (Lenanton et al. 1984). In NSW estuaries, commercial catches of some economically important species, such as *Girella tricuspidata* and *Rhabdosargus sarba*, are related to the extent of seagrass within the estuaries examined (Saintilan 2004). Other studies have documented a correlation between mangrove area and commercial fish and prawn catches (Baran 1999; Manson et al. 2005). Thus, the disappearance of nursery areas such as shallow mangrove and seagrass habitats through the construction of flood mitigation schemes could have detrimental consequences for commercial (and recreational) fisheries. Nevertheless, the contribution of different aquatic habitats to fisheries production are currently unknown and will depend on several other factors, including the natural mortality of juveniles in these habitats, the proportion of the stock size that uses these habitats, and the mortality of juveniles in the absence of these habitats.

In contrast, species assemblages in gated systems are dominated by species that are generally not associated with mangrove and seagrass habitats and that may be capable of completing their life cycles within gated systems, such as native gudgeons and the exotic eastern Gambusia. *Hypseleotris compressa*, *Philypnodon grandiceps*, and *Philypnodon* sp. 1 can complete their entire lifecycle in freshwater, whereas *Gobiomorphus australis* appears to be amphidromous (Pusey et al. 2004, and references therein). All four species deposit their eggs on solid surfaces, such as rock and wood, and in aquaria also on sand and aquatic vegetation (Pusey et al. 2004, and references therein). In gated systems the abundance of grasses and rushes and other submerged vegetation during spawning periods could thus provide ample spawning substrate and make these species self-sustaining. *Gambusia holbrooki* is a live-bearer (McDowell 1996) and could sustain itself anywhere where conditions are favourable. The presence of females with running eggs and the minimum sizes of juvenile gudgeons (*Hypseleotris compressa*, 11.9 mm; *Philypnodon grandiceps*, 7.8 mm; *Philypnodon* sp. 1, 9.6 mm; and *Gobiomorphus australis*, 8.3 mm) and eastern Gambusia (5.2 mm) in gated systems (F. Kroon, unpublished data) indeed indicate that these species do not need to emigrate to complete their life cycle.

These results support our third prediction that in gated systems, environmental conditions are not conducive to the maintenance of juveniles of economically important species. Rather, the species assemblages in gated systems are dominated by a few species, such as native gudgeons and the exotic eastern Gambusia, which are generally considered to be tolerant to disturbances (McDowell 1996; Pusey et al. 2004). The establishment of such species assemblages has been associated with decreases in environmental heterogeneity due to anthropogenic disturbance (Leidy and Fiedler 1985; Rapport et al. 1985). In the Clarence River estuary, the installation of floodgates has resulted in the removal of spatial and temporal heterogeneity in environmental conditions generally associated with tidal exchange (SPCC 1978; Pollard and Hannan 1994). Moreover, nutrient loadings in most southeast Australian estuaries have increased because of land clearing and agriculture and urban development (Roy et al. 2001). Hence, it is likely that in gated systems the construction of floodgates, increased nutrient loadings, and their interactive effects have resulted in simplification of ecosystem complexity and dominance by short-lived, opportunistic species.

In addition to environmental conditions, predator–prey relationships may influence which species do or do not occur in gated drainage systems. Invertebrate species such as *Metapenaeus macleayi*, *Palaemon debilis*, and in particular *Acetes sibogae australis* are present in large numbers and great biomass in reference systems. In Australia, *Acetes sibogae australis* has been recorded in the diet of several fish species captured during our study (*Acanthopagrus australis*, *Herklotsichthys castelnaui*, *Liza argentea*, *Platycephalus fuscus*, *Pomatomus saltatrix*, and *Rhabdosargus sarba*), as well as of many other locally occurring species of economic importance (SPCC 1981; Xiao and Greenwood 1993). Thus, the absence of large numbers and biomass of these prey species may contribute to the lack of juveniles of economically important omnivorous and carnivorous fish species in gated systems. Conversely, the low number or absence of predatory fishes in gated drainage systems may relax predation pressure, with subsequent increases in abundance and biomass of important prey species, such as native gudgeons (*Hypseleotris compressa*, *Gobiomorphus australis*, *Philypnodon grandiceps*, *Philypnodon* sp. 1) (Pusey et al. 2004, and references therein) and potentially also the exotic eastern Gambusia (*Gambusia holbrooki*).

Species assemblages (abundance and biomass) in gated and reference drainage systems are not significantly different in April and July. It is unlikely that this lack of difference is related to seasonal recruitment patterns of migrating juveniles, as juveniles of most commercially important species recruit to coastal floodplain habitats primarily in (Australian) winter months (Kroon et al. 2004). More likely, the results in April may have been related to widespread severe flooding and associated fish kills in the Clarence River in February and March (Johnston et al. 2003; Walsh et al. 2004). Severe flooding may wash recruiting juveniles out of both reference and gated systems. In addition, small fish kills were observed in some of our drainage systems in February (pH levels were within ANZECC recommended levels (ANZECC 2000), DO not available; F. Kroon, unpublished data). These fish kills have been attributed to low DO levels (Walsh et al. 2004), the causes of which were associated with drainage from acid sulfate soils and vegetation composition (Johnston et al. 2003; Walsh et al. 2004). In July, the lack of significant difference is most likely related to an extremely high abundance and biomass of *Acetes sibogae australis* in some reference and gated drainage systems (F. Kroon, unpublished data), potentially as a result of the severe flooding, and overriding any potential differences in abundance and (or) biomass of other fish and invertebrate species.

Overall, our results indicate that efforts to protect and restore coastal floodplain habitats for fisheries production should focus on improving and maintaining tidal exchange, fish passage, and water quality. First, tidal exchange and fish passage in gated drainage systems can be restored by regular and frequent opening of floodgates (see Cappo et al. 1998; Kroon et al. 2004). While Pollard and Hannan (1994) suggested that floodgates be left open permanently except "immediately prior to and during floods in the main river system", it is at these times that many species migrate across coastal floodplains (Kailola et al. 1993). The installation of tidally activated floodgates may be more practical, to remove manual dependence of opening floodgates. Second, nutrient concentrations in coastal floodplains in general, and in gated drainage systems in particular, can be reduced by a combination of more efficient fertilizer application and minimizing the loss of nutrients through runoff or leaching (Gabric and Bell 1993). We expect that the interactive effects of these management strategies across a coastal floodplain would result in the reduction of aquatic weeds and the rehabilitation of mangrove and seagrass habitats and subsequently reduce the abundance of exotic fish species and improve fisheries production.

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Persistent disturbance by commercial navigation alters the relative abundance of channel-dwelling fishes in a large river

Steve Gutreuter, Jon M. Vallazza, and Brent C. Knights

Abstract: We provide the first evidence for chronic effects of disturbance by commercial vessels on the spatial distribution and abundance of fishes in the channels of a large river. Most of the world's large rivers are intensively managed to satisfy increasing demands for commercial shipping, but little research has been conducted to identify and alleviate any adverse consequences of commercial navigation. We used a combination of a gradient sampling design incorporating quasicontrol areas with Akaike's information criterion (AIC)-weighted model averaging to estimate effects of disturbances by commercial vessels on fishes in the upper Mississippi River. Species density, which mainly measured species evenness, decreased with increasing disturbance frequency. The most abundant species — gizzard shad (*Dorosoma cepedianum*) and freshwater drum (*Aplodinotus grunniens*) — and the less abundant shovelnose sturgeon (*Scaphirhynchus platorhynchus*) and flathead catfish (*Pylodictis olivaris*) were seemingly unaffected by traffic disturbance. In contrast, the relative abundance of the toothed herrings (*Hiodon* spp.), redhorses (*Moxostoma* spp.), buffaloes (*Ictiobus* spp.), channel catfish (*Ictalurus punctatus*), sauger (*Sander canadensis*), and white bass (*Morone chrysops*) decreased with increasing traffic in the navigation channel. We hypothesized that the combination of alteration of hydraulic features within navigation channels and rehabilitation of secondary channels might benefit channel-dependent species.

Résumé : Nous présentons les premières données qui montrent que les navires commerciaux causent des perturbations chroniques de la répartition spatiale et de l'abondance des poissons dans les chenaux d'une grande rivière. La plupart des grandes rivières du globe sont aménagées de façon intensive pour accommoder les besoins grandissants du transport fluvial commercial, mais il y a peu de recherches sur l'identification et la mitigation des conséquences négatives possibles de la navigation commerciale. Afin d'évaluer les effets des perturbations causées par les navires commerciaux sur les poissons du Mississippi supérieur, nous utilisons en combinaison un plan d'échantillonnage des gradients avec des quasi-zones témoins et la pondération moyenne des modèles à l'aide du critère d'information d'Akaike (AIC). La densité des espèces, qui représente surtout l'équitabilité des espèces, diminue en fonction de la fréquence des perturbations. Les espèces les plus abondantes — l'alose à gésier (*Dorosoma cepedianum*) et le malachigan (*Aplodinotus grunniens*) — et certaines espèces moins abondantes comme l'esturgeon à museau plat (*Scaphirhynchus platorhynchus*) et la barbue à tête plate (*Pylodictis olivaris*) ne sont apparemment par affectées par les perturbations causées par le transport. En revanche, les abondances relatives des laquaiches (*Hiodon* spp.), des suceurs (*Moxostoma* spp.), des buffalos (*Ictiobus* spp.), des barbues de rivière (*Ictalurus punctatus*), des dorés noirs (*Sander canadensis*) et des bars blancs (*Morone chrysops*) diminuent en fonction de l'augmentation du trafic dans les chenaux de navigation. Nous formulons l'hypothèse selon laquelle la combinaison des modifications des caractéristiques hydrauliques dans les chenaux de navigation et de la réhabilitation des chenaux secondaires peut bénéficier aux espèces qui dépendent des chenaux.

[Traduit par la Rédaction]

Introduction

Most of the world's large rivers have been extensively altered and are subjected to a variety of anthropogenic disturbances. In response, comprehensive efforts are underway to restore ecological services provided by large rivers and to protect biodiversity (e.g., Theiling 1995; Tockner and Schiemer 1997; Pedroli et al. 2002). The efficacy of those restoration efforts depends on correct identification of both the ecological consequences of those disturbances and how any adverse consequences can be remedied. Unfortunately, rehabilitation efforts have not uniformly exploited science to maximize the probability of success (Minns et al. 1996; Lake 2001). Much remains to be learned about identification and remediation of adverse ecological consequences of alteration and anthropogenic disturbance in large rivers.

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Generally, disturbance may affect both abundance and diversity of species (Sousa 1984), and much effort has been devoted to development and testing of hypotheses about the consequences of disturbance. The intermediate disturbance hypothesis (Connell 1978) is the simplest historic theory and posits that diversity of competitors at a single trophic level is maximized at intermediate levels of disturbance. Huston's (1979, 1994) dynamic equilibrium model considers both disturbance and population growth (productivity) and predicts that diversity is maximized along a diagonal ridge between the axes of disturbance and productivity. Therefore, highly productive ecosystems such as rivers (Randall et al. 1995) may be tolerant of relatively high levels of disturbance, and the flood–pulse concept (Junk et al. 1989) postulates that a natural hydrological disturbance — periodic flooding — is the dominant driver of biological production and species interactions in floodplain rivers.

Commercial shipping is a primary use of large rivers and is projected to increase in some major systems (e.g., USACE (United States Army Corps of Engineers) 2002; Via Donau 2006). In the confined channels of rivers, large vessels can generate uniquely large physical disturbances, including sediment resuspension (Adams and Delisio 1990); altered water-velocity distributions, including flow reversals; transient changes in water-surface elevation (Bhowmik and Mazumder 1990); and changes in Reynolds stress distributions, particularly within the nearshore littoral areas (Mazumder et al. 1993).

The principal commercial vessels that ply the large rivers of the Mississippi Drainage Basin are tows, consisting of a propulsion vessel (towboat) pushing a raft of containers called barges. In the impounded portion of the Mississippi River, tows may reach 350 m in length, 32 m in width, and draft 2.7 m when fully loaded. Towboat engines can develop 2–5 MW of power and turn 2–3 propellers that may exceed 2.5 m in diameter. In that system, tow-disturbance frequencies are 1–3 orders of magnitude higher than major natural disturbances such as flooding and extreme drought.

Physical disturbances caused by shipping may have multiple acute and chronic effects on fish production in rivers (Nielsen et al. 1986; Wolter and Arlinghaus 2003). Acute effects may include mortality of larval fish from shoreline dewatering associated with vessel passage (Holland 1987) and mortality of larval (Killgore et al. 2001) and adult (Gutreuter et al. 2003) fish from entrainment through the propellers of towboats. However, the significance of entrainment mortality to population abundance and production remains unknown for lack of data on recruitment and total and fishing mortality.

Chronic, sublethal disturbance effects include altered levels of active metabolism (Rennie et al. 2005) through avoidance reactions, changes in food-resource availability, and denial of feeding and resting habitat (Wolter et al. 2005). For example, Penczak et al. (2002) speculated that low food-conversion efficiency of four species of fish in a small canal might have been the result of vessel traffic. Short-duration shoreward movements of fish during tow-passage events have been recorded in the Cumberland River (Lowery et al. 1987), and radio-tagged channel catfish (*Ictalurus punctatus*) showed transient avoidance responses to tows in the Illinois River (Todd et al. 1989). However transient movements alone are insufficient to infer whether disturbance has consequential effects on production via changes in active metabolism, food consumption, abundance, or spatial distribution.

Any persistent, chronic effects of commercial navigation and channel alteration on the distribution and production of fish in large rivers remain largely unknown. Filling that knowledge gap is a prerequisite to prediction of the consequences of any future expansion of navigation capacity. An improved understanding of the nature and mechanisms of any persistent effects of traffic or the navigation infrastructure may also help to identify effective rehabilitation tactics. This study represents an initial and prerequisite step toward that understanding. Our objectives were to (*i*) measure any differences in species density (species·(10 min)$^{-1}$) and relative abundance (fish·(10 min)$^{-1}$) between adjacent segments of a secondary and navigation channel; (*ii*) estimate the fraction of any differences that can be explained by navigation traffic; and (*iii*) identify environmental characteristics, other than traffic, that help explain any remaining differences.

Materials and methods

Study area and study design

The upper Mississippi River (UMR) spans ~1400 river km between Minneapolis, Minnesota, and the confluence of the Ohio River (Fig. 1). The UMR is a sandbed river that originally had a more complex floodplain containing braided channels and backwaters, but beginning in the 1830s, a sequence of alterations created a deepened commercial navigation channel (Anfinson 2003). The major alterations included removal of large woody debris, partial or total closure of secondary and tertiary channels to flow using weirs, installation of rock flow-deflection structures (e.g., groynes, wing dikes) that enhance hydraulic scouring of the navigation channel, and construction of 28 low-head locks and dams that have created navigation pools between Minneapolis and St. Louis, Missouri. The present navigation channel is maintained within the main channel by sporadic dredging and has a minimum low-water depth not less than 2.7 m and buoy-demarcated width generally exceeding 100 m. As a result of those alterations, fast-flowing water suitable for rheophilic fishes is now concentrated mostly within the navigation channel, where those fish are exposed to commercial navigation traffic.

Assessments of potential effects of existing navigation infrastructure and traffic on the distribution and abundance of fish are made difficult by three insurmountable limitations. First, reference data from prior to navigation are lacking, so comparisons between before and after are impossible. Second, there are no rivers — similar in all major respects other than the existence of commercial navigation — to serve as independent controls for a comparative study. For those two reasons, before–after control–impact (BACI)-type designs (Underwood 1992) are impossible. Finally, experimental manipulation of navigation traffic to help identify effects on biota is neither economically nor politically acceptable. Gradient designs (i.e., Ellis et al. 2000; Gutreuter 2004) can be effective in identification of spatially varied phenomena and are the practical means to circumvent those constraints.

We extended the conventional gradient design concept by including adjacent paired segments of secondary and main–

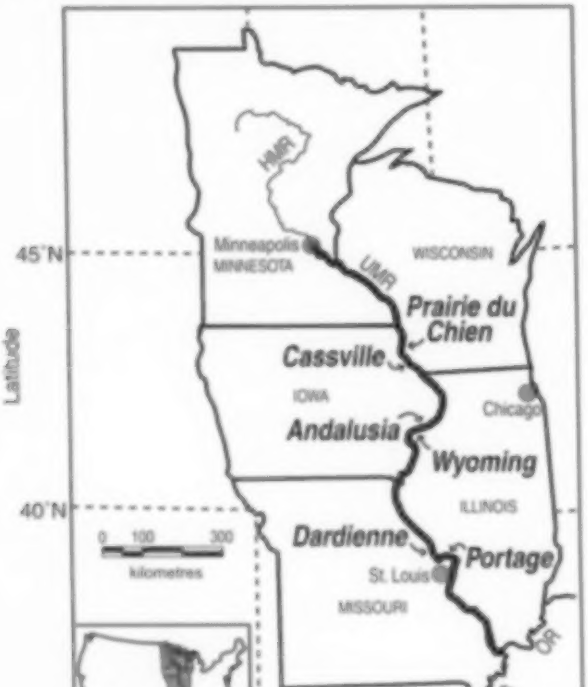

Fig. 1. The six study locations on the upper Mississippi River (UMR; inset shows location in USA) span approximately 5° of latitude. River segments: HMR, headwaters of the Mississippi River; LMR, lower Mississippi River; OR, Ohio River.

navigation channel separated by islands. We selected six study areas distributed along the present latitudinal gradient in tow-traffic frequency (Table 1). The 7-day, lagged moving average traffic frequencies ranged from 3.7 to 21.7 tows·day^{-1} along that gradient and varied approximately twofold within individual areas during our sampling. These areas are among the few remaining river segments in the UMR that contained secondary channels that approximately match the adjacent main channel in width, depth, and flow. The presence or absence of commercial navigation traffic is the principal difference between these secondary and main channel segments. Recreational vessels use both channel types. However the secondary-channel segments provided only nonindependent quasicontrols for the adjacent navigation-channel segments because both are nested within larger river segments. Fish may move among those channels within the larger river segment, so we cannot assume that all effects of traffic disturbance remain confined to the navigation channel. Further, there existed no identical matches between main and secondary channels within river segments. Simple comparisons of abundance between channel types may be due to differences in physical features other than the presence of traffic within the navigation channel. However, any differential response to the traffic gradient between secondary and navigation channels allows conservative estimation of the effect of traffic disturbance.

To fix ideas, consider hypothetical patterns in abundance from quasicontrol and impact areas, along a disturbance gradient (Fig. 2). In this simplified example, the interaction between slope and area type measures the identifiable effect of disturbance frequency on the response. Only the slope component tan(ϕ) and abundance difference c can be reasonably attributed to the effects of disturbance. Those are conservative measures of the effect of disturbance frequency because the slope tan(θ) and abundance difference a are attributable to the composite gradient, which may include some latent effects of disturbance.

Sampling and data

We sampled mainly from July through November, within the commercial shipping seasons (see supplementary material, Fig. S1[2]), during 2001 through 2003. We used daily lock-passage records (USACE 2005) as our measure of tow-traffic intensity. For each sampling date, we calculated the lagged moving averages of daily numbers of tow passages through each site for the most recent 2, 7, and 30 days. Preliminary analyses confirmed high correlations ($r^2 > 0.77$) among these three moving averages, but the 7-day moving average explained slightly more variation in fish catches. Therefore, we used the 7-day lagged moving average of daily tow passages as our measure of disturbance frequency.

We trawled within the navigation channels, as demarcated by US Coast Guard navigation buoys, and the deepest areas of secondary-channel segments within each study site to estimate the relative abundance of fish using methods described in Dettmers et al. (1999) and Gutreuter et al. (2003). The navigation channel is of interest to river managers because it is the aquatic area most directly disturbed by shipping. Our bottom trawl was constructed of 5 cm (stretch measure) nylon mesh and operated with an average wing spread of 3.9 m and average apical head-rope height of 1.2 m. We equipped the trawl with a smooth 7.6 cm diameter foot gear. Trawl distances and speeds were measured using a Raychart 420D integrated navigation and differential global positioning system (Raytheon Marine, Nashua, New Hampshire, USA). We towed the trawl upstream at an average speed of 5.5 km·h^{-1} (standard deviation, SD = 0.5 km·h^{-1}) relative to the Earth. Actual trawl times were recorded to at least the nearest 10 s. The nominal trawling effort was 15 min, measured between the times that the doors first contacted bottom upon deployment and the initiation of retrieval.

Our abundance modeling was based on 330 trawl samples that were not substantially compromised by net damage, large woody debris and other obstacles (hereafter called snags), or other untoward events. Relative abundance (catch·(10 min)$^{-1}$) provides a consistent measure for modeling and comparison among areas within the study. However,

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[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5082. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Table 1. Observed tow traffic intensity ($\bar{X}$, tows·day^{-1}) and physical dimensions of study areas in the Mississippi River.

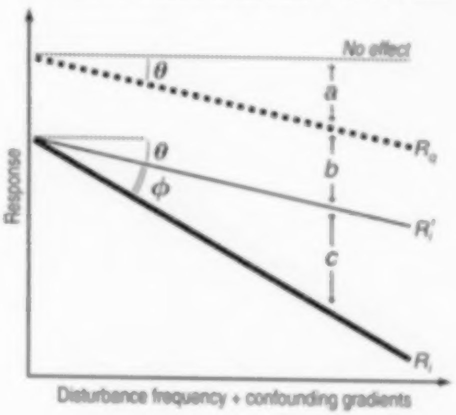
Study area	Rkm[a]	Navigation pool	$\bar{X}$ (range)	Island length (km)	Channel width[b] (m)		Mean trawl depth (m)	
					Secondary	Main	Secondary	Navigation
Prairie du Chien	1019–1024	10	5.7 (3.7–8.1)	4.6	240	170	–4.0	–5.2
Cassville	979–985	11	7.8 (5.3–9.9)	11.2	170	240	–4.3	–4.7
Andalusia	745–756	16	8.7 (6.6–10.9)	19.3	220	340	–3.5	–4.9
Wyoming	738–743	16	8.4 (6.6–10.9)	6.4	210	200	–4.2	–5.0
Dardienne	356–364	26	8.1 (5.7–13.4)	11.2	260	240	–5.4	–5.6
Portage	342–344	26	17.5 (12.7–21.7)	2.4	220	320	–5.2	–8.3

Note: Traffic intensity is the 7-day lagged moving average of daily lock passages. Island lengths and channel widths were estimated from navigation charts. The navigation channel is maintained within the trough of the main channel and is demarcated by buoys.

[a] Approximate position of the study areas in river kilometres (measured along the thalweg of the navigation channel) above the confluence of the Ohio River.

[b] Bank-to-bank.

Fig. 2. Simplified graphical model of the responses in pairs of partially separated quasicontrol and impact areas distributed along a composite gradient of disturbance frequency plus potential confounders (e.g., latitude). Suppose that the response function R_q (thick broken line) is observed from quasicontrol areas distributed along the composite gradient, wherein the slope tan(θ) is the result of effects of any composite ambient gradient. The response function R_i (thick solid line) is observed from the impact sites. The disturbance of interest occurs within the impact sites, but partial effects may also extend into the quasicontrol sites because separation is incomplete. The slope of R_i, tan(θ + ϕ), is therefore the result of the ambient gradients that also generate R_q plus the identifiable effect ϕ of the disturbance of interest within the impact sites. The slope tan(θ) and variable abundance difference *a* may be either effects of the disturbance or any confounding gradient. The response R_i' (thin solid line), having slope tan(θ), would be expected from the impact areas if they responded identically to the quasicontrols; therefore, the constant difference *b* is attributable to inherent differences between quasicontrols and impact areas. The area × gradient interaction, tan(ϕ), is attributable to the disturbance of interest unless there is also a confounding gradient that acts differently between the quasicontrols and impact sites. In our study design, potentially confounding gradients (e.g., latitude and climate, discharge, etc.) should affect the adjacent paired areas similarly, and therefore, we claim that D = disturbance frequency × tan(ϕ) is the primary presumptive effect of the disturbance. The variable difference *c* translates this effect to the scale of relative abundance.



areal estimates of population density (fish·ha^{-1}) are more easily translated for other uses. Our trawl samples swept a bottom area of approximately 0.54 ha (SD = 0.05 ha), for a sweeping rate of 0.36 ha·(10 min)$^{-1}$ (SD = 0.03 ha·(10 min)$^{-1}$). Our nominal estimates of population density are highly conservative because some fish avoid or escape from the trawl. We do not have estimates of the capture efficiency of our trawl, but estimates from elsewhere (Harley et al. 2001) range from 2% to 60%. Therefore, true population density may be 2–50 times our nominal estimates.

Our bottom trawling also provided information on the prevalence of snags that may provide habitat for fishes. We estimated snag prevalence at each site as the ratio of the number of trawl samples that encountered a major obstacle to the total number of trawl samples.

We measured the lengths of all fish to the nearest 0.1 cm using a Limnoterra IV/83/10 electronic measuring board (Limnoterra Limited, Kitchener, Ontario, Canada). We used only catch counts of fish that were at least 15 cm long for this study because (*i*) smaller fish could escape through the mesh of the trawl; (*ii*) we sought to increase precision by avoiding the high variability age-0 cohorts; and (*iii*) the "adult" stocks sustain reproduction and support commercial and recreational fisheries. Our taxonomic nomenclature follows Robbins et al. (1991).

We obtained recordings of depth (– m) at 2 s intervals, using a Garmin GPSmap 168 depth sounder (Garmin International, Olathe, Kansas, USA), along the paths of 165 trawl samples. We estimated average depth in each channel segment from those data. We calculated riverbed roughness concentration (Annambhotla et al. 1972), which is the product of the SD of depth and the wave number (m^{-1}) corresponding to the mean depth frequency and provides a measure of the flow resistance of the riverbed.

We characterized basic limnological conditions from measurements made at single index locations within each combination of site and channel type during each site visit. We measured dissolved O_2 concentrations ($mg \cdot L^{-1}$) and temperature (°C) 0.5 m below the surface using a YSI Model 57 oxygen meter (YSI Inc., Yellow Springs, Ohio, USA) and measured current velocity ($m \cdot s^{-1}$) 0.5 m below the surface, above the bottom, and at mid-depth using a Marsh–McBirney Model 2000 portable flow meter (Marsh–McBirney Inc., Frederick, Maryland, USA).

Generalized mixed-effects models for the traffic gradient

By extension of our example (Fig. 2), we formulated a set of statistical models for estimation of differences in abundance between secondary and navigation channels and the effect of navigation disturbance frequency. To avoid potential confounding with species' geographic ranges, we applied our models only to abundant species having natural geographic ranges that extended well beyond our study areas. We denote catch counts and trawling effort as C_{ij} and f_{ij}, respectively, from the *j*th trawl sample from the *i*th subject, $i = 1, \ldots, S$. A subject is the fundamental unit on which measurements are made. In our gradient design, both sites and site × channel combinations are plausible subjects. The definition of sites as subjects represents the hypothesis that fish in the adjacent channel segments form a single, intermixing population, whereas the definition of site × channel combinations as subjects represents the hypothesis that adjacent channel segments support isolated populations. We assumed that C_{ij} follow a negative binomial-normal model given by

$$(1)\quad C_{ij} | u_{ik} \sim \mathrm{NegativeBinomial}(\mu_{ij}, \delta)$$

$$\mu_{ij} = f_{ij} \exp\Big[\beta_0 + \beta_c I_c + \beta_t (T_{ij} - T_{\min}) + \beta_{tc} I_c (T_{ij} - T_{\min}) + \beta_l L_i + \beta_d D_{ij} + \beta_{ld} L_i D_{ij} + \beta_{cd} I_c D_{ij} + \beta_{cl} I_c L_i + \beta_{lcd} I_c L_i D_{ij} + \alpha_s X_{1i} + \alpha_z X_{2i} + \textstyle\sum_{k=1}^{K} u_{ik} Z_{ijk}\Big]$$

$$u_{ik} \sim \mathrm{Normal}(\boldsymbol{\theta}, \mathbf{G})$$

where u_{ik}, $k = 1, \ldots, K$, are unobserved, subject-specific, random effects having mean vector $\boldsymbol{\theta}$ and covariance matrix $\mathbf{G}$; μ_{ij} is the conditional (on the u_{ik}) mean catch; δ is the negative binomial dispersion parameter; β_0 is a constant coefficient; β_c is a parameter for the effect of the navigation channel; I_c is an indicator for channel type (0 if secondary channel and 1 if navigation channel); β_t is a parameter for the effect of recent traffic intensity T_{ij} having minimum $T_{\min}$; β_{tc} is a parameter for the differential effect of traffic intensity in the navigation channel; β_l is a parameter for the effect of standardized (mean 0 and variance 1) latitude L_i; β_d is a parameter for the effect of centered (mean 0) day of the year D_{ij}; $\beta_{ld}, \ldots, \beta_{lcd}$ are interactions, where β_{lcd} represents the differential effect of channel type on any linear seasonal response; α_s and α_z are parameters for standardized snag prevalence X_{1i} and standardized average depth X_{2i}, respectively; and $Z_{ijk} \in \{0,1\}$ is an indicator variable for the *k*th random effect. From properties of the negative binomial distribution (Lawless 1987), the within-subject variance is $\mathrm{Var}(C_{ij} | u_{ik}) = \mu_{ij} + \delta\mu_{ij}^2$, whereas for the Poisson-normal model, $\mathrm{Var}(C_{ij} | \mu_{ik}) = \mu_{ij}$. Therefore the negative binomial-normal model yields a second-order approximation to the Poisson-normal model (e.g., Lee and Nelder 2004) when $\delta = 0$. Equation 1 is said to be a conditional (on subjects), generalized mixed-effect model because it accommodates multiple observations from individual subjects by partitioning among- and within-subject variances and contains both fixed (α_s, α_z, β_0, β_c, β_t, β_{tc}, β_l, β_d, β_{ld}, β_{cd}, β_{cl}, β_{lcd}) and random effects (u_{ik}). The log-likelihood function and other model details are given in the supplementary material[2].

Any difference between channel types measured by β_c may be due to multiple causes, including the presence of traffic. Similarly, β_t may measure ancillary gradients that coincide with traffic intensity. The differential effect of traffic in the navigation channel β_{tc} is the least-confounded measure of the effect of recent tow traffic on relative abundance in the same way that the interaction between control–impact sites and before–after impact conditions provides the best evidence of impact from a BACI-type design (Stewart-Oaten and Bence 2001). We address separation of traffic effects from specific potential confounders with the inclusion effects of latitude *L*, season (day of year) *D*, specific subject-level ancillary covariates (X_{1i}, X_{2i}), and subject-specific random effects u_{ik}, which represent the set of latent variables that affect among-subject variation in C_{ik} and μ_{ij}. Preliminary analyses revealed that 60% of the variation in traffic disturbance frequency was independent of latitude. Therefore, any effects of traffic intensity on abundance could be substantially distinguished from any untoward effects of latitude. Day of the year and the interaction with latitude models any otherwise latent effects of seasonal photoperiod and temperature. Any differential movement of fish between channel types in response to seasonal photoperiod and temperature is estimated by β_{lcd}. Inclusion of that parameter aids isolation of the differential traffic response β_{tc} from any unrelated effects of latitude and season. The information content in β_{tc} is due to traffic effects when any potentially confounding factors are included in β_l, β_d, β_{ld}, β_{cd}, β_{cl}, β_{lcd}, α_s, α_z, or u_{ik}. Of course, this separation is imperfect, and therefore we claim only that β_{tc} provides the best available empirical evidence for any chronic effect of tow traffic in the absence of any ability to identify traffic effects via experimental manipulation of multiple identical rivers.

We quantified the differences between channel types and the traffic-disturbance effect using three functions of eq. (1). The marginal (integrated over all subjects) mean difference in relative abundance between secondary and navigation channel, at the mean values of the other covariates, is given by

$$(2)\qquad \hat{\Delta C}_{S-N}\, f^{-1} = \exp\left[\hat{\beta}_0 + \hat{\beta}_t(t - t_{\min}) + \frac{1}{2}\hat{\sigma}_u^2\right] \times \{1 - \exp[\hat{\beta}_c I_c + \hat{\beta}_{tc} I_c (t - t_{\min})]\}$$

for $T = t$ and where $\hat{\sigma}_u^2$ is the estimate of the random-effect variance (see supplemental material[2]). This is the overall mean difference between the channel types regardless of cause and, by analogy, measures the vertical distance $b + c$ (Fig. 2). The direct, presumptive, multiplicative effect of traffic-disturbance frequency on abundance in the navigation channel is given by

$$(3)\qquad \hat{D} = \exp[\hat{\beta}_{tc}(t - t_{\min})]$$

which is the fraction by which baseline (at $T = t_{\min}$) abundance changes when $T = t$. Corresponding to the vertical distance c (Fig. 2), the predicted marginal mean difference in relative abundance in the navigation channel between disturbance frequencies t and $t_{\min}$ is given by

$$(4)\qquad \hat{\Delta C}_{\Delta N}\, f^{-1} = \exp\left[\hat{\beta}_0 + \hat{\beta}_c I_c + \hat{\beta}_t(t - t_{\min}) + \frac{1}{2}\hat{\sigma}_u^2\right](\hat{D} - 1)$$

The quantity $\hat{\Delta C}_{\Delta N}\, f^{-1}$ is a less-precise measure of the effect of traffic-disturbance frequency than $\hat{D}$ because its variance is additionally a function of the variances and covariances of $\hat{\beta}_0$, β_t, $\hat{\beta}_{tc}$, and $\hat{\sigma}_u^2$. However, $\hat{\Delta C}_{\Delta N}\, f^{-1}$ translates $\hat{D}$ to relative abundance and is more easily interpreted.

We fitted a total of eight variations of eq. 1 to identify patterns in relative abundance that are robust over a range of modeling assumptions. First, we assigned both sites and site × channel-type combinations as subjects. For each choice of subjects, we fitted models that assumed a first-order autoregressive (AR[1]) process over years, having variance $\sigma_u^2 = \sigma_{AR}^2$ and autoregression parameter ρ and a single random effect having variance $\sigma_u^2 = \sigma^2$. Finally, for each of the four resulting combinations, we fitted models that include and exclude the ancillary covariates for snag prevalence and mean depth.

Model averaging and comparison

We had little interest in identification of a best model from the set. Rather, we incorporated model uncertainty using model averaging of β_0, β_c, β_t, β_{tc}, $\hat{\delta}$, and eqs. 2–4 based on Akaike weights (Buckland et al. 1997; Burnham and Anderson 2002).

To further check the utility of the gradient-design parameters β_0, β_c, β_t, and β_{tc}, we compared results with the same eight variations on more highly saturated reference models containing categorical effects of navigation pool and channel type through the conditional mean-response function

$$(5)\qquad \mu_{ij} = f_{ij}\exp\Big[\beta_0 + \beta_c I_c + \sum\nolimits_{l=1}^{3}(\beta_p I_l + \beta_{pc} I_p I_c) + \beta_l L_i + \beta_d D_{ij} + \beta_{ld} L_i D_{ij} + \beta_{cd} I_c D_{ij} + \beta_{cl} I_c L_i + \beta_{lcd} I_c L_i D_{ij} + \alpha_s X_{1i} + \alpha_z X_{2i} + \sum\nolimits_{k=1}^{K} u_{ik} Z_{ik}\Big]$$

where, for $p = 1,\ldots,3$, the β_p and β_{pc} are a total of six parameters for the effects of four navigation pools and navigation channels within pools, respectively, the I_p are three indicator variables for the four pools, and the remaining parameters are as in eq. 1. These reference models are not constrained by the traffic-gradient parameters β_t and β_{tc}. Hence, they provide the means to identify any alternatives to that gradient that may better represent the data.

Results

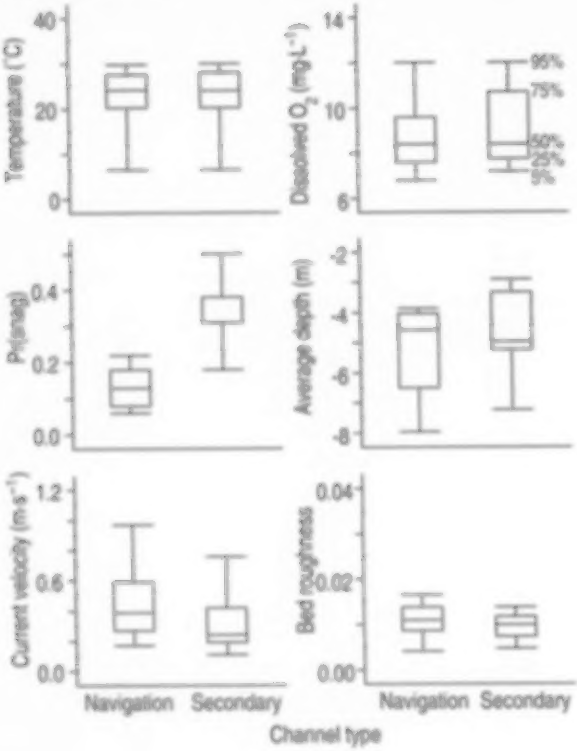
Abiotic similarities between channel types

The navigation and secondary channel segments in our study areas were generally similar. Because flow was separated by relatively small islands, physical and chemical characteristics of the water such as temperature, dissolved oxygen concentrations, and Secchi transparencies (not shown) were essentially identical between secondary and navigation channels (Fig. 3). Median trawl depths differed by less than 0.5 m, but the extremes from the secondary channels tended to be less than those from the navigation channels. The greatest depth mismatch occurred at Portage Island, where the mean depth of the navigation channel was greater than any other study area (Table 1). Current velocities and bed roughness values were only slightly greater in the navigation channels than in the secondary channels (Fig. 3). The most pronounced difference we detected was in the prevalence of snags, mainly large woody debris, which we encountered approximately twice as often in secondary channels than in the navigation channel.

Comparison of fish community characteristics

We caught 44 species (supplementary material, Table S1[2]). Secondary and navigation channels generally supported fish communities having similar species compositions. Only the rheophilic shovelnose sturgeon (*Scaphirhynchus platorhynchus*) and silver chub (*Macrhybopsis storeriana*) were more prevalent and abundant in the navigation channel than in the secondary channels, whereas several taxa, including gizzard shad (*Dorosoma cepedianum*), common carp (*Cyprinus carpio*), the buffaloes (*Ictiobus* spp.), catfishes (*Ictalurus* spp., and *Pylodictus olivarus*), white bass (*Morone chrysops*), pike–perches (*Sander* spp.) and freshwater drum (*Aplodinotus grunniens*) were distinctly more prevalent and abundant in the secondary channels. Our trawl caught relatively large fishes, and the small cyprinids were notably absent. The length distributions of abundant species were generally similar between secondary and navigation channels, except for freshwater drum, for which juveniles were distinctly more prevalent in the secondary channels than in the navigation channels, and *Hiodon* spp., for which juve-

Fig. 3. Distributions of physical factors in the secondary and navigation channels.

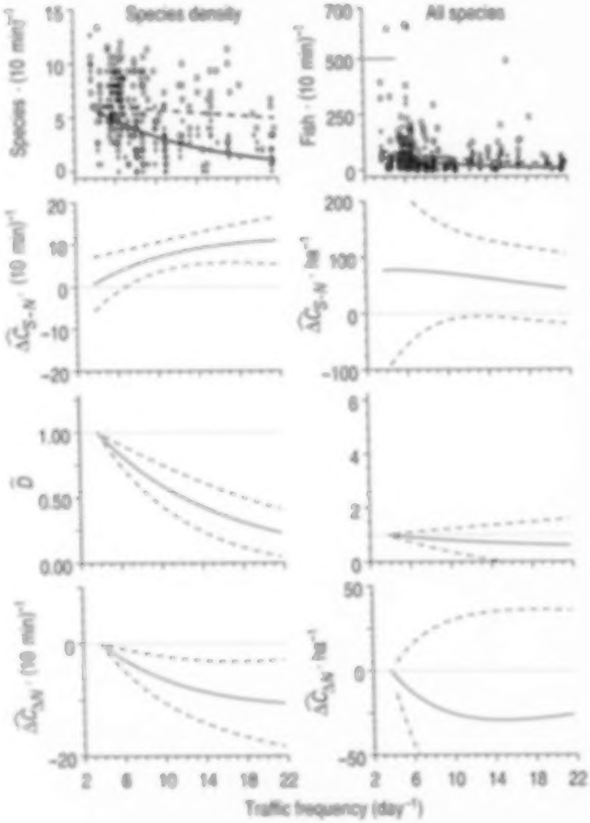


niles were more abundant in the navigation channels (supplementary material, Fig. S1[2]).

Species density decreased along the composite traffic gradient and tended to be greater in the secondary-channel than in the navigation-channel segments; the 90% point-wise prediction intervals on the mean difference $\Delta\hat{C}_{S-N}$ in species density between secondary and navigation channel excluded zero for traffic intensities >7 tows·day^{-1} (Fig. 4). A navigation-traffic disturbance frequency of 13 tows·day^{-1} is expected to reduce species density in the navigation channel by approximately 50%, and 90% prediction intervals on $\hat{D}$ excluded 1.0 over all disturbance frequencies >4 tows·day^{-1}. Similarly, the predicted species-density difference in the navigation channel between the presence and hypothetical absence of traffic disturbance, $\Delta\hat{C}_{\Delta N}$, was consistently less than zero. Latitude, measured by β_l, had no separately identifiable effect on species density, and there was no evidence for any differential seasonal response between channel types, measured by $\beta_{c,d}$ (Appendix Table A1).

The areal density of all fishes of all species decreased along the composite traffic gradient and was greater in secondary channels only in the lower end of the gradient (more northerly latitudes). The total areal density was unaffected by traffic disturbance frequency as measured by $\hat{D}$ and $\Delta\hat{C}_{\Delta N}$ (Fig. 4). However, total fish densities tended to be greater in secondary channels than in the navigation channel in areas where traffic intensity exceeded 10 tows·day^{-1}. That difference was driven, in part, by a channel-specific effect of latitude, as measured by $\beta_{c,l}$ (Appendix Table A1).

Fig. 4. Model-averaged summaries for species density (sample-wise species richness) and the total abundance of all fishes. The upper panels display the observed and marginal mean counts C from secondary (open circles and broken lines, respectively) and navigation channels (pluses and solid lines, respectively) per 10 min of trawl effort. $\Delta\hat{C}_{S-N}$ is the predicted marginal mean difference between secondary and navigation channels and is defined by eq. 2. $\hat{D}$ is the dimensionless, multiplicative, presumptive effect of traffic disturbance on counts in the navigation channel and is defined by eq. 3. $\Delta\hat{C}_{\Delta N}$ is the predicted marginal mean difference between counts from the navigation channel in the presence and absence of the presumptive traffic effect and is defined by eq. 4. For $\Delta\hat{C}_{S-N}$, $\hat{D}$, and $\Delta\hat{C}_{\Delta N}$, solid lines are the predicted marginal means, and broken lines are 90% prediction intervals.



Effects of channel type and disturbance frequency on the prevalent taxa

Among the most prevalent species, model-averaged mean relative abundance within the navigation channel tended to decrease along the composite disturbance–frequency gradient, except for shovelnose sturgeon, for which mean relative abundance increased slightly with traffic frequency only in the secondary channel segments (Fig. 5). The population

Fig. 5. Observed and model-averaged predicted marginal mean catch rates (fish·(10 min)$^{-1}$) of prevalent fishes in secondary (open circles and broken lines) and navigation (pluses and solid lines) channels of the upper Mississippi River.

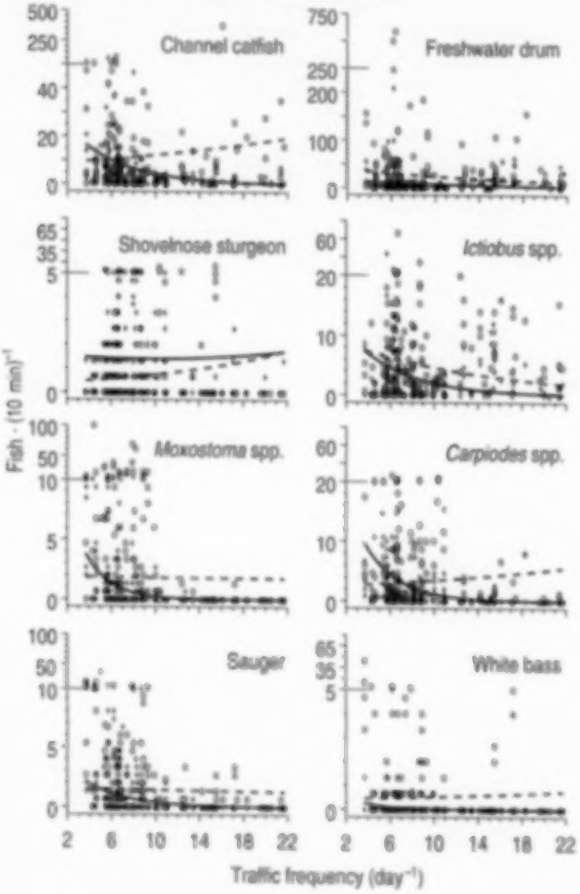
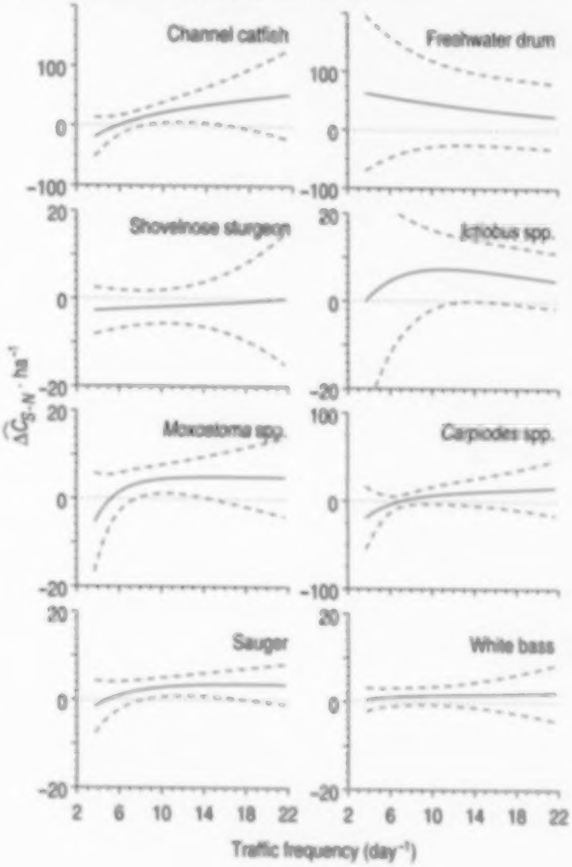


Fig. 6. Model-averaged marginal mean difference in population density (fish·ha^{-1}) between secondary and navigation channels (solid lines) and 90% prediction intervals (broken lines). $\Delta\hat{C}_{S\text{-}N}$ is defined by eq. 2 and is conservative because an unknown fraction of fish avoided capture by our trawl.



densities of channel catfish, buffaloes, redhorses (*Moxostoma* spp.), and sauger (*Sander canadensis*) were identifiably greater in the secondary channels than in the navigation channels over at least some portion of the composite gradient (Fig. 6). Any differences in population densities of freshwater drum, shovelnose sturgeon, carpsuckers (*Carpiodes* spp.), and white bass between channel types were not resolved.

Tow-traffic disturbance affected the relative abundances of channel catfish, the buffaloes, redhorses, carpsuckers, sauger, and white bass, but not gizzard shad (not shown), flathead catfish (*Pylodictis olivaris*, not shown), or freshwater drum within the navigation channel (Fig. 7). Our analyses indicate that within the navigation channel, disturbance frequencies exceeding 9 tows·day^{-1} reduced the mean relative abundances of channel catfish, redhorses, carpsuckers, sauger, and white bass to less than 50% of expected values at the minimum observed traffic frequency of $t_{\min}$ = 3.7 tows·day^{-1}. Any response by shovelnose sturgeon was poorly resolved for lack of precision or nonexistent. Our models predict reductions in channel catfish population densities of at least 50 fish·ha^{-1} for disturbance frequencies exceeding 10 tows·day^{-1} (Fig. 8). For the buffaloes, redhorses, and sauger, the largest reduction in density due to traffic disturbance occurred at disturbance frequencies of 10–18 tows·day^{-1}. However, in contrast with the more precise measure $\hat{D}$, the 90% prediction intervals on $\Delta\hat{C}_{\Delta N}$ for those species included zero over the range of the data. Consistent with $\hat{D}$, there was no evidence that traffic disturbance reduced the navigation-channel population densities of freshwater drum. Despite the large fractional reductions in the relative abundance of white bass as measured by $\hat{D}$, the predicted differences in their population densities associated with disturbance frequency $\Delta\hat{C}_{\Delta N}$ were trivially small (Fig. 8) because their relative abundances were generally low (Fig. 5).

There was no evidence of any identifiable effect of latitude on relative abundance, except for the redhorses and sauger, which tended to be more abundant at more northerly

Fig. 7. Model-averaged, presumptive, multiplicative effect of traffic disturbance, $\hat{D} = \exp(\hat{\beta}_{tr}\, t)$, on abundance of prevalent fishes in the navigation channels of the upper Mississippi River (solid lines) and 90% confidence intervals (broken lines).

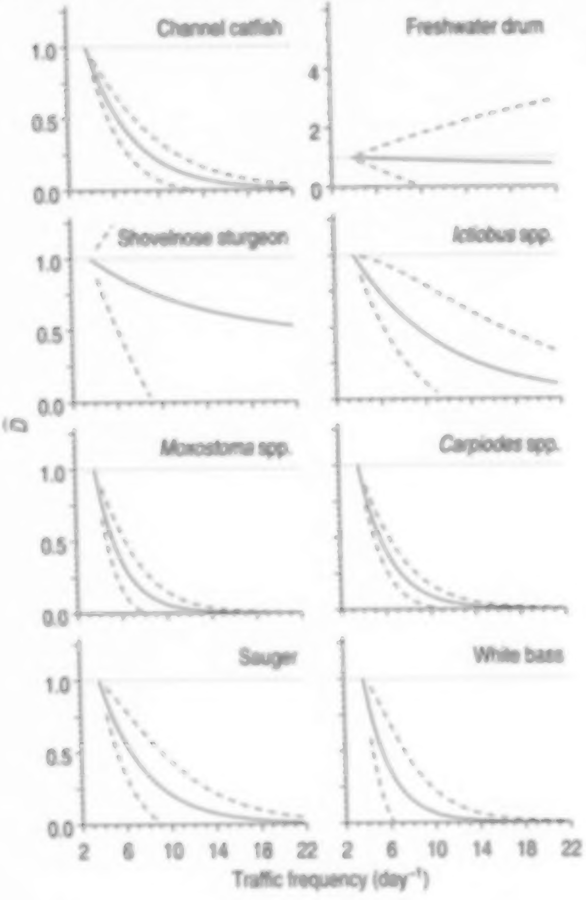
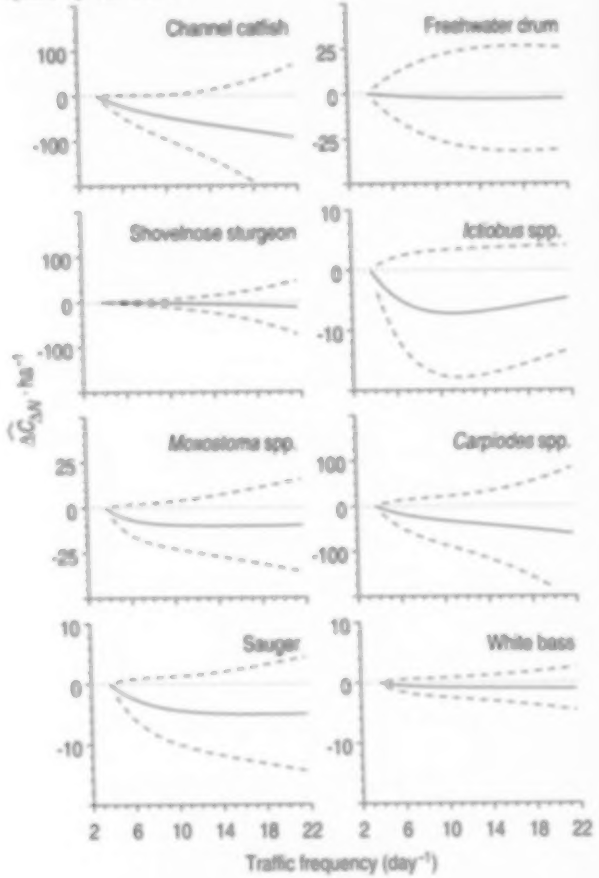


Fig. 8. Model-averaged, marginal mean predicted difference in population density (fish·ha^{-1}) of prevalent fishes in the navigation channel of the upper Mississippi River with and without the presumptive traffic effect (solid lines) and 90% prediction intervals (broken lines). The prediction function $\Delta\hat{C}_{\Delta N}$ is defined by eq. 4 and is conservative because an unknown fraction of fish avoided capture by our trawl.



latitudes ($\hat{\beta}_l$ − 2 standard errors (SE) > 0; Appendix Table A1). The catch rates of the toothed herrings (*Hiodon* spp.), gizzard shad, the carpsuckers, buffaloes, redhorses, catfishes, white bass, and sauger increased from summer through autumn ($\hat{\beta}_d$ − 2SE > 0), and that response varied with latitude for gizzard shad, the toothed herrings, carpsuckers, redhorses, and flathead catfish ($|\hat{\beta}_{ld}| > 2SE$). More importantly, there was no evidence of any preferential concentration in either channel type associated with the onset of movement to overwintering habitat during our sampling ($|\hat{\beta}_{tr,d}| < 2SE$).

Serial correlation, population structuring, and the importance of the covariates

Although our primary interest was in inference after accounting for model uncertainty using model averaging, patterns in the relative performances of the eight models aided interpretation and provided additional insights. For any combination of ancillary covariate status (included, excluded) and subject definition (site, site × channel), models that included the AR[1] random-effect variance structure always yielded smaller Akaike's information criterion (AIC; smaller is better; Burnham and Anderson 2002) values than models containing a constant random-effect variance. Accommodation of serial correlation seems generally important.

Inclusion of the site × channel (versus site) subject effect was the next most important factor distinguishing the better models. For at least three of the four combinations of ancillary covariate status and random-effect variance structure, models that included site × channel combinations as subjects yielded smaller AIC values than models that included sites as subjects for flathead catfish, freshwater drum, gizzard shad, sauger, the buffaloes, white bass, and the total catch. Conversely, models that included sites as subjects were superior in at least three of four combinations only for the carpsuckers. Although navigation and secondary channel segments are separated only by islands, these results suggest that there was relatively little mixing of fish between those segments during the times of our sampling.

The inclusion of the ancillary covariates for snag prevalence and average depth seemed relatively unimportant. For any combination of subject definition and random-effect variance structure, models for the toothed herrings, sauger, and white bass that excluded snag prevalence and average depth always yielded smaller AIC values than models that included both covariates. In contrast, inclusion of snag prevalence and average depth always yielded better models for the buffaloes, freshwater drum, and total catch. The model-averaged parameter estimates and SEs (Appendix Table A1) provide evidence of positive associations between snag prevalence and the relative abundances (α_s – 2SE > 0) of the buffaloes. The species densities and the relative abundances of the carpsuckers, buffaloes, freshwater drum, and all species combined showed evidence of increase with greater depth (α_d + 2SE < 0).

Reality checking by comparisons with the reference models

The reference models that replaced the composite traffic gradient with gradient-free, river-reach identifiers (eq. 5) were generally uncompetitive, as measured by AIC, with the gradient models (eq. 1). However, the reference models for shovelnose sturgeon and freshwater drum outperformed (smaller AIC) the gradient models by mean AIC differences of 6 and 14, respectively. For all other taxa, the gradient models outperformed the reference models by mean AIC differences of 10 to 63.

Discussion

The results of this study suggest that high-frequency disturbance (>6–8 tows·day^{-1}) from river towboats has measurable consequences to the spatial distribution and local magnitudes of species density and the abundance of certain fishes of the Mississippi River. However, those effects apparently do not translate into effects on fish species richness, because that has been constant, except for the addition of exotics, for at least decades (Coker 1929; Fremling et al. 1989). The historic constancy of species richness in the UMR is at odds with simplistic predictions of both the intermediate disturbance hypothesis (IDH; Connell 1978) and the dynamic equilibrium model (DEM; Huston 1994). Under the IDH, we should expect to have observed a long-term decline in species richness. Wooton's (1998) results provide at least a partial explanation for the constant species richness in the UMR: the IDH may apply only to species competing for relatively static basal resources. Given the high productivity of this system, increased species richness would be consistent with the DEM. However, increases in species richness are constrained by the rates of speciation and invasion. Further, there is no standard by which to measure disturbance, and multiple factors are important in heterogeneous ecosystems such as large floodplain rivers. The IDH and DEM may have posterior descriptive value, but may be insufficient to generate predictions that are useful to the management of complex ecosystems. Therefore, it seems more pragmatic to evaluate the consequences of disturbance to individual species or guilds in these ecosystems.

It is useful to speculate why some species seem to be affected by tow-traffic disturbance while others do not. The specialization–disturbance (S–D) hypothesis (Vázquez and Simberloff 2002) posits that specialists — species having narrow niche breadth — are more sensitive to disturbance than generalists through either effects on population stability (Morin and Lawler 1996) or spatial range restrictions (Brown 1984). In the context of the present study, higher sensitivity to traffic disturbance among channel specialists than habitat generalists would be consistent with the S–D hypothesis. Among the four species that showed little or no evidence of response to tow-disturbance frequency, only the shovelnose sturgeon are rheophils and flathead catfish are fluvial specialists. The abundances of seven taxa — the toothed herrings, carpsuckers (dominated by *C. carpio* and *Cyprinus cyprinus*), buffaloes (dominated by *Ictiobus bubalus*), redhorses (dominated by *Moxostoma macrolepidotum*), channel catfish, white bass, and sauger — were inversely related to traffic-disturbance frequency. Our buffaloes and redhorses are fluvial specialists. Although channel catfish, sauger, and white bass adapt well to lentic environments, these species are largely fluvial specialists within the UMR. The toothed herrings are fluvial limnetic specialists, having some affinity for strong gradients in current velocity that occur mainly in channels. However, the carpsuckers are largely fluvial generalists. Therefore, our observational study provides only weak and equivocal support for the S–D hypothesis. Although we did not seek to identify specific causal mechanisms, our results suggest that deeper inquiry into behavioral responses and life-history traits will be needed to predict and test responses to various disturbances.

The total abundance of all species of fish and abundances of dominant species, including gizzard shad and freshwater drum, were seemingly unaffected by tow-traffic frequency in our study areas of the UMR. However, species density was reduced within the navigation channel with increasing tow-traffic frequency as measured by both $\widehat{\Delta C}_{\Delta N}$ and $\hat{D}$. Because we encountered nearly all of the same species in both channel types (supplementary material, Table S1[2]), species density reflects species evenness rather than species richness. Thus, although traffic-disturbance frequency does not seem to affect total abundance of fish, it does seem to reduce species evenness, perhaps by reducing the abundance of less common species.

The estimates $\hat{D}$ and $\widehat{\Delta C}_{\Delta N}$ seem to conflict for the buffaloes, redhorses, carpsuckers, sauger, and white bass. However, that conflict is easily resolved. The $\hat{D}$ is the more primary and precise measure of tow-disturbance frequency because it is a function of the single parameter estimate $\hat{\beta}_{N}$. In contrast, $\widehat{\Delta C}_{\Delta N}$ translates $\hat{D}$ to the scale of population density through multiple model parameters and is therefore more variable than $\hat{D}$. Finally, the largest values of $\hat{D}$ typically occurred where low levels of relative abundance constrained $\widehat{\Delta C}_{\Delta N}$ to small values. Thus, although the point-wise 90% prediction intervals on $\widehat{\Delta C}_{\Delta N}$ always included zero for those species, it would be incorrect to conclude that $\widehat{\Delta C}_{\Delta N}$ contradicted any information provided by $\hat{D}$. For example, it is clear that abundance of redhorses within the navigation channel was reduced to less than 10% of baseline relative abundance when traffic frequency reaches approximately 9 tows·day^{-1}, although some additional replications of our sampling would indicate that population density (fish·ha^{-1}) is not reduced for lack of precision in the estimation of $\widehat{\Delta C}_{AN}$.

The estimates $\hat{D}$ and hence $\widehat{\Delta C}_{AN}$ likely underestimate the effects of tow-traffic disturbance on fishes for two reasons. First, $\hat{D}$ may not capture all effects of disturbance because some of those effects remain confounded in $\hat{\beta}_c$, which by analogy measures the difference b in Fig. 2. Second, unbiased estimation of D requires that the channel types are identical except for the presence of tow traffic. Although we sampled from the best matches present, the unusual depth of the navigation channel at Portage Island may have introduced a conservative bias. Tow-traffic frequencies were greatest in that channel segment; therefore, that site has a high degree of leverage on parameter estimates. However, the atypical depths provide resident benthic fishes with an equally atypical vertical separation from the hulls and propellers of tows, which may decrease the frequency of avoidance reactions in that channel segment.

Some taxa differed in abundance between large secondary channels and the navigation channel in ways that suggest management strategies for large rivers. For example, species density and the relative abundances of channel catfish, the buffaloes, redhorses, and sauger tended to be distinctly greater in the secondary channels than in the navigation channels, at least over some intervals of traffic-disturbance frequency. Those results suggest that maintenance and enhancement of relatively free-flowing secondary channels, especially where traffic intensity is high, may benefit the production of those and perhaps other species.

Large woody debris is undeniably important to some lotic fishes because it structures predator–prey interactions and provides shelter and substrate for the production of food organisms (Crook and Robertson 1999). For those reasons, restoration of large woody debris may provide means to increase production (Bond et al. 2006). Snag (principally large woody debris) prevalence was the most obvious distinguishing physical difference between channel types that we were able to measure. However, the ratios of the model-averaged estimates of the snag-prevalence parameter to its standard error were less extreme than 2.0 for all taxa except the buffaloes, which showed a positive association with snag prevalence. Oddly, the model-averaged snag-prevalence parameter was unimportant for the cover-seeking channel and flathead catfishes. Although our estimates of the snag-prevalence parameter suggest minimal importance, part of the effect of large woody debris is confounded with channel type and therefore remains imbedded in the overall difference in abundance between secondary and navigation channels.

Rheophilic fishes are likely to be responsive to spatial patterns in flow velocity. For example, Wildhaber et al. (2003) found associations between meso-scale abundance of some channel-dwelling fishes and some statistical summaries of bedforms. River bedforms and flow interact to create variable but predictable patterns in near-bottom flow velocity. For example, the leeward faces of sand dunes that approach the angle of repose create areas of flow separation (Haque and Mahmood 1985) that may provide bioenergetic refuges for fish (Guensch et al. 2001). Further, we hypothesize that the same forces that result in flow separation and the selective sorting of sediment particles based on mass (Mazumder et al. 2005) may also create hydraulic traps that allow the accumulation of macroinvertebrate drift within bedform troughs and that any such trapping may increase the foraging efficiency of invertebrate-feeding fishes. Our depth measurements were sufficient to estimate roughness concentration (Annambhotla et al. 1972) with reasonable precision, but (unpublished) simulations showed that our instruments lacked the spatial resolution and temporal frequency needed to estimate the slopes of bedform faces. Therefore, our depth recordings lack sufficient resolution to distinguish areas of high and low flow separation, and additional research will be needed to identify any preferential selection of specific bedform features by rheophils.

Changes in relative abundance due to disturbances from tows have at least three plausible causes. First, disturbance by towboats may induce transient avoidance reactions. The present study was not designed to measure such transient reactions. Although the results of Todd et al. (1989) indicate that transient avoidance reactions occur in channel catfish, the energetic costs of those reactions are unknown. Second, mortality may result when some fish are entrained through the propellers of towboats. In the UMR, non-zero entrainment mortality rates were estimated for shovelnose sturgeon, gizzard shad, skipjack herring (*Alosa chrysochloris*), and smallmouth buffalo (*Ictiobus bubalus*) (Gutreuter et al. 2003). The results of the present study do not refute the hypothesis that entrainment mortality has a minor effect on the abundance of shovelnose sturgeon. Last, high-frequency disturbances may result in persistent partial abandonment of otherwise suitable habitat. That abandonment might occur as a direct result of avoidance reactions that have a higher energetic cost than can be met within the navigation channel or as an indirect result of alterations to food quantity or availability.

The energetic costs of high-frequency disturbance may be ecologically consequential. For example, the metabolic costs of elevated activity may result in reduced somatic growth rates even when more food resources are available to highly active populations (Rennie et al. 2005). Elevated activity costs may have broader indirect effects on populations and communities where early growth influences the flux of juveniles to the adult stock (Gutreuter and Anderson 1985) and because the von Bertalanffy growth parameter k provides an indirect measure of reproductive investment and is also interrelated with total mortality rate (Shuter et al. 2005). We believe that it would be worthwhile to measure the metabolic costs of tow-induced avoidance reactions using in situ electromyogram telemetry calibrated against laboratory respirometry (Standen et al. 2002; Healey et al. 2003).

River rehabilitation has become a substantial industry in the United States (Bernhardt et al. 2005) and Europe (Buijse et al. 2002). In the UMR, rehabilitation efforts have been mandated by a law stating that "a nationally significant ecosystem and a nationally significant commercial navigation system is maintained" (USACE 2004). Forty rehabilitation projects were completed by the Environmental Management Program of the Upper Mississippi River System through 2003. Only 10 of those projects included some form of rehabilitation of secondary channels, but interest in channel-dwelling biota is increasing with recognition of their potential vulnerability (Galat and Zweimüller 2001). If physical resources are limiting to populations, then river rehabilitation efforts may be an effective way to enhance biological production and biodiversity. If another resource (e.g., food) is limiting, then rehabilitation efforts that fail to substantially augment that resource are unlikely to yield measurable returns. Unfortunately, both on the UMR system (Gutreuter 2004) and other rivers worldwide (Buijse et al. 2002; Bernhardt et al. 2005), science to support rehabilitation design and evaluation is sorely lagging behind the pace of construction. Frequently, there is too little scientific information about ecosystem function and limiting factors to predict which management strategies are likely to maximize the return on investment.

The present study is suggestive of some river rehabilitation possibilities that could serve as hypotheses for adaptive management (Walters 2001) of large rivers, but does not provide a rigorous test of limiting factors. The increased species density and relative abundance in large secondary channels certainly suggests better environmental quality there than in the navigation channel for some fishes. If limiting resources are more abundant in large secondary channels than in the main channel, then rehabilitation of occluded secondary channels or creation of new ones (Grift et al. 2003) would increase the production of rheophilic fish populations and perhaps increase species evenness at small spatial scales. Our results also clearly suggest that high-frequency navigation disturbance alters at least the spatial distribution and perhaps population size and production of some species. Unfortunately, we can only pose hypotheses about the underlying mechanisms of those biological responses to disturbance. Given the present uncertainty about any population-level consequences of entrainment mortality (Gutreuter et al. 2003), we hypothesize that production of shovelnose sturgeon and perhaps other rheophils would benefit from any rehabilitation strategies that exploit hydraulic cues to attract them out of the navigation channel and into the main-channel borders or secondary channels. The feasibility of any such rehabilitation strategies requires a far better knowledge of the specific factors that attract and support those species. For other species (e.g., channel catfish and sauger), there is no evidence of entrainment mortality. Their patterns of abundance were likely the consequence of sublethal behavioral responses to tow traffic. Those species tended to be more abundant in the secondary channels. We hypothesize that their expenditures on active metabolism are lower in secondary channels than in navigation channels having high tow-disturbance frequencies. Further, we hypothesize that production of their food resources is also greater in secondary channels than in frequently disturbed navigation channels. Finally, we hypothesize that experimental restoration of permanent flow in a sufficiently large, occluded secondary channel, within a reach otherwise devoid of flowing secondary channel, would result in measurable increases in population size and production of those species.

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Appendix A

Appendix appears on the following page.

Table A1. Model-averaged parameter estimates (standard errors) obtained from the sets of models used to identify effects of disturbance

Taxon	β_0	β_y	β_v	β_w	β_t	β_d	β_{td}	β_{vd}
Shovelnose sturgeon	−1.2173 (0.7370)	0.0673 (0.0807)	1.0387 (0.8662)	−0.0586 (0.1135)	−0.0707 (0.3098)	−0.0117 (0.2564)	−0.4197 (0.1311)	0.3324 (0.3261)
Hiodon spp.	−1.3532 (0.7886)	0.1228 (0.0988)	−0.3300 (1.3824)	−0.2932 (0.1491)	−0.2424 (0.5020)	1.7055 (0.3244)	0.4001 (0.1650)	−1.6667 (0.4511)
Gizzard shad	2.3338 (1.4973)	−0.5635 (0.1665)	−0.8483 (2.3311)	−0.1729 (0.2122)	−0.9794 (0.8214)	2.7872 (0.4073)	0.3671 (0.1911)	−0.1483 (0.6120)
Carpiodes spp.	0.1843 (0.7854)	0.0423 (0.0617)	1.3206 (0.5476)	−0.3814 (0.0607)	0.5923 (0.2516)	0.8659 (0.1876)	−0.1458 (0.0898)	−0.6140 (0.2560)
Smallmouth buffalo	1.5887 (0.4526)	−0.0799 (0.0480)	0.0765 (0.8308)	−0.1132 (0.0677)	0.2429 (0.2684)	0.1782 (0.1399)	−0.1579 (0.0707)	−0.0892 (0.2092)
Ictiobus spp.	1.7768 (0.4585)	−0.0768 (0.0478)	0.0000 (0.8260)	−0.1280 (0.0670)	0.1595 (0.2684)	0.2252 (0.1374)	−0.1793 (0.0692)	−0.1091 (0.2028)
Moxostoma spp.	0.2268 (0.4780)	−0.0025 (0.0712)	0.7019 (0.7285)	−0.4428 (0.1256)	0.9378 (0.1731)	0.5334 (0.2634)	0.2400 (0.1485)	−0.4030 (0.4014)
Channel catfish	1.8701 (0.3299)	0.0390 (0.0430)	0.5312 (0.3406)	−0.2508 (0.0468)	−0.2041 (0.1380)	0.6487 (0.1240)	0.0530 (0.0627)	−0.3661 (0.1762)
Flathead catfish	−1.1191 (0.3222)	0.0224 (0.0407)	−0.7024 (0.6117)	−0.0710 (0.0696)	−0.0968 (0.1507)	0.8303 (0.1586)	0.1203 (0.0782)	−0.0536 (0.2586)
White bass	−1.3192 (0.7557)	0.0199 (0.0973)	−0.5357 (1.3113)	−0.4436 (0.2073)	0.5031 (0.3710)	1.6014 (0.4007)	−0.0873 (0.2192)	−0.2421 (0.8788)
Sauger	−0.0002 (0.3786)	−0.0088 (0.0511)	0.3168 (0.6376)	−0.2528 (0.0982)	0.3290 (0.1462)	0.8951 (0.1951)	0.0733 (0.0994)	−0.4018 (0.3033)
Freshwater drum	2.6077 (0.6241)	−0.0641 (0.0601)	−1.0242 (1.0916)	−0.0154 (0.0849)	0.2533 (0.3922)	1.0847 (0.1640)	−0.1246 (0.0739)	−0.1172 (0.2339)
Total catch	4.1466 (0.3478)	−0.0722 (0.0381)	−0.3952 (0.5807)	−0.0412 (0.0575)	0.1570 (0.1891)	0.9115 (0.1086)	0.0233 (0.0489)	−0.1488 (0.1626)
Species density	1.7758 (0.1659)	1.7758 (0.1659)	−0.0417 (0.2905)	−0.0837 (0.0274)	0.0711 (0.0879)	0.2966 (0.0444)	−0.0038 (0.0189)	0.0480 (0.0752)

Note: See text for descriptions of the parameters.

*Averaged over only the four models containing the parameter. All other parameter estimates were averaged over all eight models.

frequency on relative abundance and species density.

$\beta_{c,d}$	$\beta_{h,d}$	α_1^*	α_2^*	δ	σ^{2*}	$\sigma^2_{AR}{}^*$	ρ^*
0.4178 (0.3015)	0.1556 (0.1758)	0.2064 (0.5145)	0.4261 (0.5750)	1.5494 (0.2412)	0.7223 (0.5134)	0.8988 (0.4938)	0.8988 (0.4836)
0.3366 (0.5161)	–0.3374 (0.2380)	–1.7898 (0.7759)	1.3560 (0.7568)	2.0781 (0.4145)	0.4057 (0.3690)	1.2205 (0.6570)	1.2205 (0.6786)
–0.6225 (0.8753)	–0.0796 (0.3085)	1.3233 (1.4023)	–2.2032 (1.1240)	2.5273 (0.3417)	4.9623 (3.0626)	6.0287 (2.3314)	6.0287 (0.3452)
–0.6140 (0.1930)	–0.0559 (0.1389)	0.5032 (0.2631)	–0.6215 (0.3044)	0.9225 (0.1235)	1.3967 (0.8651)	1.5179 (0.8366)	1.5179 (0.3295)
–0.6617 (0.2717)	–0.1518 (0.1041)	0.8060 (0.3921)	–0.8332 (0.3177)	1.2633 (0.1412)	0.1724 (0.1343)	0.3963 (0.1634)	0.3963 (0.4359)
–0.5898 (0.2696)	–0.1326 (0.1010)	0.8186 (0.3876)	–0.8634 (0.3162)	1.1418 (0.1269)	0.1635 (0.1304)	0.3905 (0.1610)	0.3905 (0.4210)
–0.6289 (0.2543)	–0.0771 (0.2131)	–0.0803 (0.5301)	0.2004 (0.4657)	1.3992 (0.1920)	0.0049 (0.0063)	0.7716 (0.4322)	0.7716 (0.2937)
–0.1586 (0.1187)	–0.0249 (0.0871)	0.0599 (0.2656)	–0.2051 (0.3058)	1.3379 (0.1256)	0.0000 (0.0002)	0.7757 (0.3526)	0.7757 (0.3142)
–0.1630 (0.2177)	–0.0102 (0.1303)	0.4488 (0.4167)	–0.4107 (0.3515)	0.4396 (0.1783)	0.0958 (0.1212)	0.3855 (0.2024)	0.3855 (0.3323)
–0.4446 (0.5242)	–0.1430 (0.4928)	–0.8199 (1.1581)	0.6459 (1.2891)	2.4114 (0.5485)	0.4418 (0.3646)	0.9564 (0.6345)	0.9564 (0.5278)
–0.1708 (0.2106)	0.2171 (0.1473)	0.0462 (0.4471)	–0.0853 (0.3860)	0.9081 (0.1506)	0.0878 (0.1020)	0.8189 (0.3827)	0.8189 (0.2728)
–0.6438 (0.3949)	0.0481 (0.1139)	0.8351 (0.6966)	–1.1715 (0.4895)	1.3347 (0.1230)	0.6627 (0.5099)	1.8630 (0.6013)	1.8630 (0.2767)
–0.4055 (0.1799)	–0.1280 (0.0702)	0.6624 (0.3200)	–0.7484 (0.2585)	0.7430 (0.0608)	0.0167 (0.0397)	0.5244 (0.2118)	0.5244 (0.2757)
–0.1756 (0.0919)	–0.0486 (0.0300)	0.2334 (0.1440)	–0.2271 (0.1142)	<0.0001 (<0.0001)	0.0397 (0.0277)	0.0958 (0.0354)	0.0958 (0.3632)

Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*)

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Abstract: We used our long-term annual bottom trawl survey (1973–2004) in Lake Michigan to reveal the response of the native fish community to the biological control of a dominant exotic fish, alewife (*Alosa pseudoharengus*), as well as to changes in total phosphorus and salmonine biomass. Through nonmetric multidimensional scaling, we documented a 1970s community largely dominated by alewife, and then a shift to a community dominated by several native species during the 1980s through 1990s, when alewife remained at relatively low levels. We argue that the recovery of burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsonii*), and yellow perch (*Perca flavescens*) was partially or fully aided by the alewife reduction. We argue that changes in phosphorus or salmonines were not directly related to abundance increases of native species. An additional community shift occurred during 1999–2004, which coincided with a reduction in species richness and total fish biomass in our trawl. The mechanisms underlying this latest shift may be related to reductions in nutrients, but further research is required. The restoration of the native fish community has been incomplete, however, as emerald shiner (*Notropis atherinioides*), cisco (*Coregonus artedii*), and lake trout (*Salvelinus namaycush*) have yet to demonstrate recovery.

Résumé : Nos données d'inventaire à long terme de chalutage de fond (1973–2004) dans le lac Michigan nous servent à présenter la réaction de la communauté de poissons indigènes à la lutte biologique contre le gaspareau (*Alosa pseudoharengus*), une espèce exotique dominante, ainsi qu'aux changements de phosphore total et de biomasse des salmoninés. Par cadrage multidimensionnel non métrique, nous décrivons dans les années 1970 une communauté fortement dominée par le gaspareau, puis un glissement durant les années 1980 jusqu'à la fin des années 1990 vers une communauté dominée par plusieurs espèces indigènes, alors que les gaspareaux maintiennent des densités relativement faibles. Nous pensons que la récupération de la lotte (*Lota lota*), du chabot de profondeur (*Myoxocephalus thompsonii*) et de la perchaude (*Perca flavescens*) a été favorisée en partie ou en totalité par la réduction des gaspareaux. Nous croyons que les changements observés dans le phosphore et chez les salmoninés ne sont pas reliés directement aux augmentations d'abondance des espèces indigènes. Il s'est produit un nouveau glissement de communauté en 1999–2004, qui a coïncidé avec une réduction de la richesse spécifique et de la biomasse totale des poissons dans nos prélèvements au chalut. Les mécanismes explicatifs de ce dernier glissement peuvent être associés à la diminution des nutriments, mais il faudrait plus de recherches pour le confirmer. La récupération de la communauté de poissons indigènes n'est cependant pas complète, cependant, car le méné émeraude (*Notropis atherinioides*), le cisco de lac (*Coregonus artedii*) et le touladi (*Salvelinus namaycush*) ne montrent pas encore de signes de restauration.

[Traduit par la Rédaction]

Introduction

Ecologists and managers are becoming increasingly familiar with the negative consequences (e.g., decline of native species, habitat degradation) of dominant nonnative species (hereafter, exotic) on communities and ecosystems. When management attempts to eradicate or control exotic species are successful (see Myers et al. 2000 for a review), monitoring and research of the long-term effects on the restoration of native species are relatively rare (Zavaleta et al. 2001). In freshwater ecosystems, for example, efforts to eliminate exotic salmonids from streams or small lakes (through cessation of stocking, management removal, or scientists conducting manipulative experiments) has been a common approach, but the post-removal monitoring of the aquatic community generally ranges 2–6 years (e.g., Harig and Bain 1998; Lintermans

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2001; Sarnelle and Knapp 2004). These studies revealed that native fish (Harig and Bain 1998; Lintermans 2001; Peterson et al. 2004) and frog (Vredenburg 2004) species can indeed gain short-term increases in abundance as a result of the exotic fish removal. For those systems that became fishless after the removal, some zooplankton species that did not occur prior to the removal reappeared (Parker et al. 2001; Sarnelle and Knapp 2004). Other zooplankton taxa, however, failed to reappear within the course of the study (Parker et al. 2001; Sarnelle and Knapp 2004).

Determining the longer-term effects of exotic fish removal or control on native species restoration has generally occurred by revisiting a system with a single survey 7–30 years after the intervention (e.g., Donald et al. 2001; Knapp et al. 2001). These post-intervention snapshots have revealed that zooplankton (Parker et al. 1996; Donald et al. 2001; Knapp et al. 2001) as well as benthic macroinvertebrate and frog (Knapp et al. 2001) populations can recover to pre-fishless conditions. These recoveries, however, may take up to 19 years (Donald et al. 2001), and not all diatom (Drake and Naiman 2000) and zooplankton (Parker et al. 1996) species are restored. In total, both short-term (≤6 years) annual monitoring and longer-term snapshots following the reduction or removal of an exotic fish have demonstrated the capacity of some native species to be restored. The ability to generalize this result and make longer-term predictions of the effect on native communities, however, will require replication of these reductions or removals of exotics across systems as well as longer-term annual monitoring than has currently been achieved (Knapp et al. 2001).

The Laurentian Great Lakes have endured the invasion of more than 140 exotic species since the early 1800s, including more than 25 exotic fishes (Mills et al. 1993; Ricciardi and MacIsaac 2000). Several of these exotic fishes have had tremendous ecological and economic impacts on the Great Lakes, including the sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseudoharengus*), and Chinook salmon (*Oncorhynchus tshawytscha*; Mills et al. 1993). In Lake Michigan, alewife were first observed in 1949 perhaps taking advantage of the sea lamprey's near elimination of the top native predator (i.e., lake trout, *Salvelinus namaycush*) that may have otherwise prevented a successful invasion (Smith 1970). Over the next 20 years, the alewife population progressively increased in size until massive die-offs began to occur in the mid-1960s, which led to blockages in industrial and municipal water intakes and economic hardship for tourism because of alewife carcasses littering the southern beaches (Brown 1972). From an ecological perspective, alewife consumption of native fish larvae and competition with native young-of-year fishes for limited zooplankton are believed to have resulted in the decline of several native fish species, including the deepwater sculpin (*Myoxocephalus thompsonii*; Madenjian et al. 2005*a*), emerald shiner (*Notropis atherinoides*; Crowder 1980), cisco (also known as lake herring, *Coregonus artedii*; Smith 1970; Wells and McLain 1973), and yellow perch (*Perca flavescens*; Wells 1977; Jude and Tesar 1985; Eck and Wells 1987), and have limited the restoration of lake trout (Krueger et al. 1995).

Partially owing to the economic and ecological hardship wrought by the alewife, state management agencies launched a salmonine (i.e., lake trout, Chinook salmon, coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*)) stocking program in Lake Michigan in the mid-1960s in an attempt to initiate top-down control of alewives, restore the native lake trout, and initiate a valuable sport fishery (Madenjian et al. 2002). It was not feasible to attempt to eradicate alewife, largely because of the size of Lake Michigan and an alewife life history that includes high fecundity and an early age at maturity (i.e., by age 3; Norden 1967). Annual salmonine stocking has been maintained to present, and we will present data to demonstrate that salmonine biomass increased through the mid-1980s, until it declined as a result of a disease outbreak, but then returned to mid-1980s levels by the 2000s.

Although using biological control (i.e., using an exotic species to control another abundant exotic species) often fails and can even have negative consequences on the ecosystem (Williamson 1996; Simberloff and Stiling 1996), the use of salmonines to control alewife abundance has been largely successful to date. Because alewife is their primary diet item (Stewart and Ibarra 1991; Madenjian et al. 1998), salmonine predation on alewife was the primary mechanism underlying the decline of alewife biomass in the 1970s and early 1980s (Madenjian et al. 2005*b*). Over the past 20 years, alewife biomass has trended neither upward nor downward and remained at a low level compared with the 1960s and early 1970s (Madenjian et al. 2005*b*). Several papers have quantitatively evaluated the effect of alewife abundance on specific native fish populations (e.g., Shroyer and McComish 2000; Madenjian et al. 2005*a*; Bunnell et al. 2006), but none have quantitatively evaluated the effect on the fish community as a whole.

Herein, we have the unique opportunity to evaluate the longer-term response of the Lake Michigan fish community to the decline of a dominant exotic species with annual surveys. Specifically, we apply a multivariate analysis to a bottom trawl time series spanning from 1973 to 2004 to describe the long-term shifts in the fish community. By 1982, the alewife population could be considered under control, as adult biomass was estimated to be less than 10% of its peak biomass in 1966 (Madenjian et al. 2005*b*), and it remained at less than 10% for 19 of the next 22 years (exceptions: 15% in 1998, 15% in 2002, 14% in 2003). In addition to the potential effect of the alewife decline on the fish community, we explore the potential effect of changing lake productivity and salmonine biomass as other factors that could be contributing to the observed fish community changes.

Materials and methods

Field sampling

Since 1973, the Great Lakes Science Center (GLSC) has conducted an annual bottom trawl survey for prey fish at seven fixed ports (Frankfort, Michigan; Ludington, Michigan; Manistique, Michigan; Port Washington, Wisconsin; Saugatuck, Michigan; Sturgeon Bay, Wisconsin; Waukegan, Illinois) around the perimeter of Lake Michigan. In some years, however, some ports were not sampled because of weather or boat problems: Port Washington in 1976, Manistique in 1995, 2001, and 2002. In 1998, all ports were sampled but we do not use data from that year because the trawl was towed at an unusually fast speed (4.7 km·h^{-1}), which affected catchability. We also do not use data from 2000 because only three ports were sampled. At each port, a transect of on-contour sites was fished at up to 11 different depth strata, ranging between 9 and 110 m with ~9 m increments. Because of bottom topography, not all depths could be sampled at all ports.

For the duration of the survey, GLSC fished a ¾ Yankee Standard No. 35 bottom trawl (12 m headrope, 15.5 m footrope, and a 13 mm mesh in the cod end). Towing speed averaged 3.4 km·h^{-1}, and most tows were generally 10 min in duration. When the entire catch was less than about 20 kg, fish were sorted by species, counted, and an aggregate species weight was measured. In larger catches, conspicuous larger species (i.e., age 1 and older burbot (*Lota lota*), channel catfish (*Ictalurus punctatus*), common carp (*Cyprinus carpio*), freshwater drum (*Aplodinotus grunniens*), gizzard shad (*Dorosoma cepedianum*), lake whitefish (*Coregonus clupeaformis*), longnose sucker (*Catostomus catostomus*), round whitefish (*Prosopium cylindraceum*), white sucker (*Catostomus commersonii*), yellow perch (*Perca flavescens*)) and all lake trout were removed, and then a random sample of 10–15 kg was selected for species sorting, counting, and aggregate weighing. The remainder of the inconspicuous catch was then weighed for later extrapolation of the sorted sample. Since 1976, the fin clip (or absence thereof) has been noted for all lake trout captured. Hatchery-reared, fin-clipped lake trout have been stocked in Lake Michigan annually since 1965 (Holey et al. 1995).

We calculated annual mean biomass density (kg·ha^{-1}) for each species through a series of steps. First, we summed the biomass density for each species in each tow (i.e., at each depth stratum) and then performed a natural log(x + 1) transformation to reduce the skewness of the distribution. Next, we calculated the mean biomass density for each species in each depth stratum across ports. Finally, the annual, species-specific mean biomass density was calculated as a weighted mean density across depth strata, where the area of each depth stratum was the weight. Because the fish populations that we analyzed had different depth distributions, a weighted mean was a more accurate index of their population biomass within our sampling area (i.e., Lake Michigan depths between the 5 and 114 m depth contours) than was an unweighted mean.

Analyses

For all analyses, we excluded some species for two reasons. First, we did not include species that were caught in only 2 or fewer years of the time series (e.g., sea lamprey, rainbow trout, brown trout, walleye (*Sander vitreus*), spoonhead sculpin (*Cottus ricei*), round goby (*Neogobius melanostomus*), white perch (*Morone americana*), white bass (*Morone chrysops*), Chinook salmon, bluegill (*Lepomis macrochirus*)). Because no species were caught in only 3, 4, or 5 years of the time series, we included all species that were caught in at least 6 years of the time series. Second, we excluded the threespine stickleback (*Gasterosteus aculeatus*) because this nonnative species was first collected in Lake Michigan in 1984 (Stedman and Bowen 1985), during the middle of the time series. Since 1984, it has been collected in all but 3 years of the survey. In total, we focused on the biomass density patterns of 20 species (Table 1). We calculated species richness (i.e., total number of species captured) for each year of the time series.

To determine whether biomass density patterns differed across species that occupy different depths of the lake, we assigned each species to either a nearshore (<30 m), intermediate (30–70 m), or offshore (>70 m) habitat (Table 1). To assign a habitat, we calculated the weighted mean depth of capture for each species in each year, where the weight equaled the mean biomass density for each depth strata. The mean of the annual weighted mean depths was used to assign habitat.

To determine annual shifts in fish community composition, we used nonmetric multidimensional scaling (NMS; Kruskal 1964; Mather 1976), a nonparametric ordination technique. It is an iterative process that seeks to minimize the "stress" of a k-dimensional configuration. Unlike many other ordination techniques, NMS is well suited for nonnormal data, avoids the assumption of linear relationships among variables, and allows the use of any distance measure (McCune and Grace 2002). Hence, it has become increasingly popular for ecological data sets (e.g., Ault and Johnson 1998; Beisner et al. 2003; Zamon and Welch 2005). To calculate the dissimilarity matrix, we used the Sørenson (Bray–Curtis) distance measure (Clarke 1993; McCune and Grace 2002). We chose not to relativize the data, because we wanted true differences in species biomass to be included. In the end, we had a matrix consisting of 30 years × 20 species.

To implement NMS, we used the "slow and thorough" autopilot mode of the PC-ORD software (MjM Software Design, Gleneden Beach, Oregon), which determines the minimum stress value from 40 runs for up to six-dimensional configurations. It also performs a Monte Carlo test of 50 runs of randomized data to determine whether the solution is providing significantly more (α = 0.05) reduction in stress than expected by chance. To avoid overfitting the data and (or) a local minimum solution, we checked for the stability of the ordination by ensuring that the standard deviation of stress was less than 0.000 010 over the final 15 iterations.

To understand which species biomass densities were driving the ordination on each axis, we correlated the ranks of axis scores and species biomass density with Kendall's τ. Because we conducted 20 correlations on each axis (i.e., one of each species), we used a Bonferroni adjustment of the significance level (α = 0.0025) to maintain an overall α = 0.05. We used cluster analysis to form groups of years of similar species composition within the ordination. To be consistent with the NMS ordination, we used a Sorensen's distance matrix and flexible beta linkage (also known as flexible clustering) where β = –0.25 (McCune and Grace 2002). The dendrogram was scaled by Wishart's objective function converted to percentage of information retained. Our goal was to minimize the number of groups while maximizing the percentage of information retained.

To explore the potential effects of salmonine biomass and lake productivity on changes in the fish community, we correlated their respective time series with each of the axis scores using Kendall's τ. To construct a time series for salmonine biomass, we relied on two sources. To estimate lake-wide biomass of Chinook salmon, we used the same statistical catch-at-age model (i.e., Benjamin and Bence 2002) described in Madenjian et al. (2002), but used updated harvest

Table 1. Summary of fishes captured during autumn bottom trawl survey that were used in analysis.

Common name	Scientific name	Mean depth (m)	Habitat	Years
Alewife	*Alosa pseudoharengus*	60 (55–64)	Intermediate	30
Bloater	*Coregonus hoyi*	60 (56–64)	Intermediate	30
Burbot	*Lota lota*	53 (46–59)	Intermediate	22
Channel catfish	*Ictalurus punctatus*	14 (10–17)	Nearshore	12
Common carp	*Cyprinus carpio*	14 (11–16)	Nearshore	19
Deepwater sculpin	*Myoxocephalus thompsonii*	96 (95–98)	Offshore	30
Freshwater drum	*Aplodinotus grunniens*	18 (12–24)	Nearshore	6
Gizzard shad	*Dorosoma cepedianum*	19 (11–27)	Nearshore	18
Johnny darter	*Etheostoma nigrum*	34 (30–38)	Intermediate	29
Lake trout	*Salvelinus namaycush*	43 (39–47)	Intermediate	30
Lake whitefish	*Coregonus clupeaformis*	33 (26–41)	Intermediate	29
Longnose sucker	*Catostomus catostomus*	29 (20–39)	Nearshore	23
Ninespine stickleback	*Pungitius pungitius*	49 (44–53)	Intermediate	30
Rainbow smelt	*Osmerus mordax*	45 (41–48)	Intermediate	30
Round whitefish	*Prosopium cylindraceum*	21 (18–24)	Nearshore	26
Slimy sculpin	*Cottus cognatus*	79 (75–82)	Offshore	30
Spottail shiner	*Notropis hudsonius*	16 (12–19)	Nearshore	29
Trout-perch	*Percopsis omiscomaycus*	23 (20–26)	Nearshore	30
White sucker	*Catostomus commersonii*	15 (11–19)	Nearshore	22
Yellow perch	*Perca flavescens*	18 (16–20)	Nearshore	30

Note: Mean depth is the grand mean of the annual weighted mean depth of capture; 95% confidence limits of annual mean depths are in parentheses. Habitat was determined by mean depth: nearshore (<30 m), intermediate (30–70 m), offshore (>70 m). Years equals the number of years (of 30) in which the fish were collected during the survey.

and age data to produce a revised estimate of Chinook salmon biomass through 2003. To estimate Chinook biomass in 2004, we used the average biomass of years 2001–2003. To estimate lake-wide biomass of lake trout, brown trout, rainbow trout, and coho salmon, we used the previously published time series described in Madenjian et al. (2002), which included years up to 1999. Unfortunately, lake-wide data to update the models of these other species from Madenjian et al. (2002) were unavailable. Hence we calculated the average biomass for each species during 1997–1999 and then applied those values to 2000–2004. Our time series of salmonine biomass equaled the annual sum of the aforementioned species.

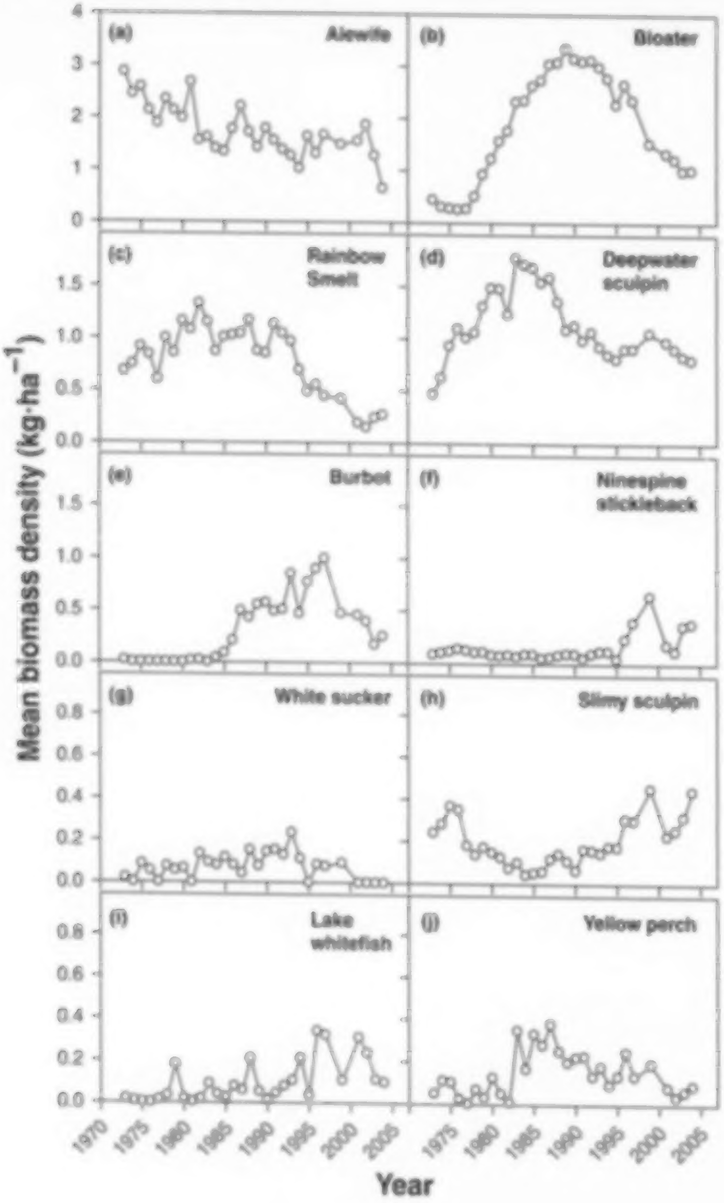
To construct time series of Lake Michigan productivity, we also relied largely on previously published data. One potential surrogate for productivity is the external loadings of total phosphorus to the Lake. Madenjian et al. (2002) provided a loadings time series spanning 1974–1995, with missing years in 1992 and 1993. Because the loadings time series has not been updated, we assumed that loadings in 1996–2004 equaled the average of the loadings in 1994–1995. To fill in the other missing years, we assumed that loadings estimated in 1974 equaled the loadings from 1973 and that the loadings in 1992–1993 equaled the mean of the 1990, 1991, and 1994 loadings. A better measure of lake productivity is measured total phosphorus concentrations in the lake. Unfortunately, as discussed in Madenjian et al. (2005*b*), complete time series of measured phosphorus concentrations in the offshore, and especially in the nearshore, sites of Lake Michigan spanning 1973–2004 do not exist. As a result, we used the spring total phosphorus time series constructed by Madenjian et al. (2005*b*), which covers 1974–1999. To expand the time series to 2004, we assumed that their phosphorus concentrations in 2001–2004 equaled the mean of the phosphorus concentrations in 1997–1999.

Results

Annual mean biomass density available to the bottom trawl was dominated by alewife, bloater (*Coregonus hoyi*), deepwater sculpin, and rainbow smelt (*Osmerus mordax*) in all years of the survey (Figs. 1*a*–1*d*). Alewife dominated the biomass until 1981, after which bloater became the predominate species through 1999. Between 2002 and 2004, either alewife or bloater dominated the time series biomass. Of the 16 remaining less common species, seven different ones had the greatest mean biomass density over the course of the time series (burbot, common carp, lake trout, lake whitefish, ninespine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*), yellow perch). We present biomass time series for six of these seven species (Figs. 1*e*–1*j*), as well as the four dominant species (Figs. 1*a*–1*d*), as these 10 species all were correlated with axis scores from the ordination in our results below.

Grouping species by depth habitat, all groupings displayed a loose unimodal distribution with a variable but increasing trend early in the time series followed by a variable but decreasing trend late in the time series (Figs. 2*a*, 2*b*, 2*d*). Because alewife and bloater dominated the biomass in the intermediate depth habitat (i.e., 30–70 m), we removed those

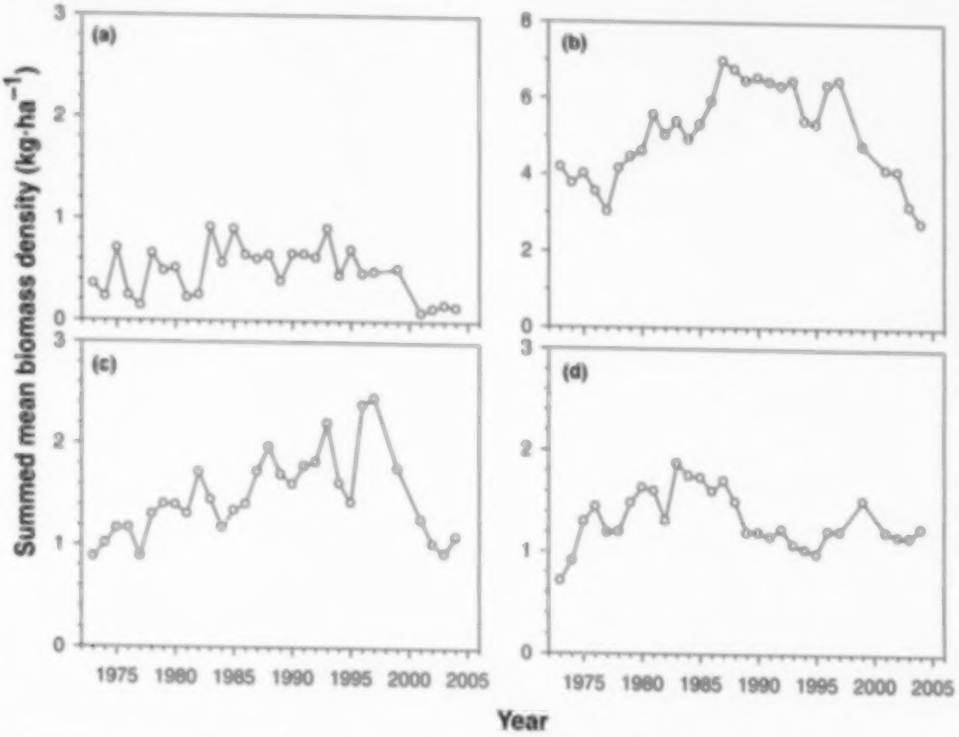
Fig. 1. Mean biomass density (kg·ha^{-1}) time series of log(x + 1)-transformed bottom trawl data for 10 of the most commonly captured species. Note differences in y-axis scales among rows of panels.



species and still found this loose unimodal distribution to occur (Fig. 2*c*). Similar to the biomass trends, the time series of species richness indicated a variable but increasing trend in species richness early in the time series, followed by a period of relatively high richness, and then a decline in richness in the 2000s (Fig. 3). The increase in species richness in the mid-1980s was primarily associated with the collection of burbot, freshwater drum, and channel catfish. The decline in species richness after 1999 was primarily due to the absence of channel catfish, common carp, gizzard shad, freshwater drum, and white sucker from the survey trawls. The most consistent pattern among these figures is the general decline in both mean species biomass density in all habitats as well as species richness in the last 5 or so years of the survey.

The occurrence of lake trout without a fin clip (indicating that it was naturally reproduced) was rare. Since 1976, we have captured 984 lake trout in the bottom trawl survey and only 10 individuals, or 1.0%, were unclipped. Given that an expected frequency of unclipped lake trout of greater than

Fig. 2. A time series of the summed mean biomass density (kg·ha^{-1}) of log(x + 1)-transformed bottom trawl data for fish species grouped by depth habitat: (*a*) nearshore species (<30 m), (*b*) intermediate species (30–70 m), (*c*) intermediate species (30–70 m) excluding bloater (*Coregonus hoyi*) and alewife (*Alosa pseudoharengus*), and (*d*) offshore species (>70 m). See Table 1 to discern which species comprised each depth habitat.



5% would be indicative of some degree of natural reproduction (Madenjian et al. 2004), our survey provided no evidence for natural reproduction of lake trout.

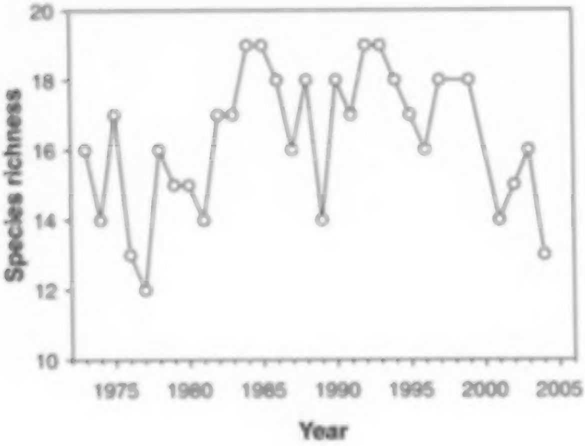
For the multivariate analysis, a two-dimensional representation was identified by PC-ORD as providing a sufficiently stable and low stress value (7.36) while not overfitting the data (Fig. 4). These two axes explained 96% of the variation in the data, as measured by the coefficient of determination between the Euclidean distances in ordination space and Sorensen distances in the original species space. We trimmed the dendrogram from the cluster analysis at four groups, which retained about 30% of the information. Each group corresponded to a consecutive set of years. Using correlations between the ranks of axis scores and species biomass density, we identified which species were most associated with an area of each axis (Fig. 4). For example, alewife biomass density was negatively correlated (i.e., $P < 0.0025$) with NMS axis 2 scores. As a result, we could describe the species that were most associated with each group of years identified from the cluster analysis.

The 1973–1978 cluster (Fig. 4) represented a period of domination of fish biomass by alewife (Fig. 1*a*), ranging from 39% to 55% of the total mean biomass density. The ordination of this cluster was positively correlated with densities of alewife, as well as slimy sculpin and ninespine stickleback, both of which exhibited higher biomass densities during these years than during the 1980s (see Figs. 1*h* and 1*f*, respectively). This cluster was associated with relatively low densities of several native species, including bloater, burbot, deepwater sculpin, lake whitefish, white sucker, and yellow perch. The 1979–1982 cluster (Fig. 4) represented a period where alewife biomass density began to decline (24%–36% of the total biomass density; Fig. 1*a*), and several native species began to increase their densities, most notably bloater (Fig. 1*b*) and deepwater sculpin (Fig. 1*d*). Finally, another exotic species, rainbow smelt, had generally been increasing since 1973 but reached its first and third highest biomass densities of the time series during the 1979–1982 cluster (Fig. 1*c*).

The 1983–1997 cluster was a period dominated by the native bloater (Fig. 1*b*), which represented 28%–41% of the total mean biomass density over this time period. Including 15 years, this cluster stretches over a large part of the ordination and is more easily described by focusing on two different sets of years within the cluster. First, several native species attained their highest biomass density of the time series during the 1980s subset of the cluster, including bloater, deepwater sculpin (Fig. 1*d*), and yellow perch (Fig. 1*j*). In the 1990s subset of the cluster, another suite of native species, burbot (Fig. 1*e*), lake whitefish (Fig. 1*i*), and white sucker (Fig. 1*g*), exhibited their highest biomass density of the time period. Exotic rainbow smelt exhibited a general decline during the 1990s, as did deepwater sculpin and yellow perch.

The fourth and final cluster included 1999–2004, and its axis scores were associated with lower densities of several of the native species that had peaked during the 1980s or

Fig. 3. Species richness time series estimated from the US Geological Survey Great Lakes Science Center Lake Michigan bottom trawl survey.



1990s, including bloater, deepwater sculpin, white sucker, and yellow perch. Additionally, exotic alewife and rainbow smelt remained at relatively low densities. Two native species, however, slimy sculpin and ninespine stickleback (Figs. 1*h* and 1*f*, respectively), attained their highest mean biomass density of the time series during these years. This cluster was also associated with relatively high densities of lake whitefish and burbot, despite lower mean densities during 1999–2004 than during the previous 3 years.

To explore whether changes in salmonine biomass (Fig. 5*a*) or lake productivity (Fig. 5*b*) over the time period were related to the fish community shifts, we correlated their respective time series with each of the axis scores. Salmonine biomass was unrelated to either axis ($P > 0.9$). Both measures of productivity, external phosphorous loadings and phosphorus concentrations in the lake, were negatively correlated to axis 2 ($r = -0.59$, $P < 0.0001$; and $r = -0.59$, $P < 0.0001$, respectively), which indicates that the shifts in the 1973–1982 clusters to the 1983–2004 clusters coincided with a reduction in phosphorus in Lake Michigan.

Discussion

As exotic species become more dominant within ecosystems, managers will be increasingly called upon to consider eradication or control efforts towards the exotics. To facilitate that decision process, however, managers will require information regarding the successes and failures of previous efforts in similar systems. In freshwater ecosystems, previous studies have documented either the short-term (i.e., 4–7 years), with annual monitoring, or long-term (i.e., >10 years), with a snapshot survey, response of the native community to the management effort (e.g., Harig and Bain 1998; Knapp et al. 2001; Sarnelle and Knapp 2004). In this paper, however, we provided the results of an annual survey that documented the long-term response of the native fish community to the biological control of exotic alewife. We found unique clusters of fish communities in the 1980s through 2000s to be correlated with high densities of several native fish species, as opposed to a cluster in the 1970s that was correlated with high densities of exotic alewife. Below, we argue that the restoration of at least three of these species (i.e., burbot, deepwater sculpin, yellow perch) was aided by alewife control; the recovery of some of the other native species (i.e., bloater, lake whitefish) was likely influenced by factors other than alewives. We also discuss the potential effect of other perturbations in Lake Michigan that may have been influencing the fish community during this time period, such as declines in total phosphorus, changes in salmonine biomass, as well as the introduction of exotic dreissenid mussels (i.e., zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*)).

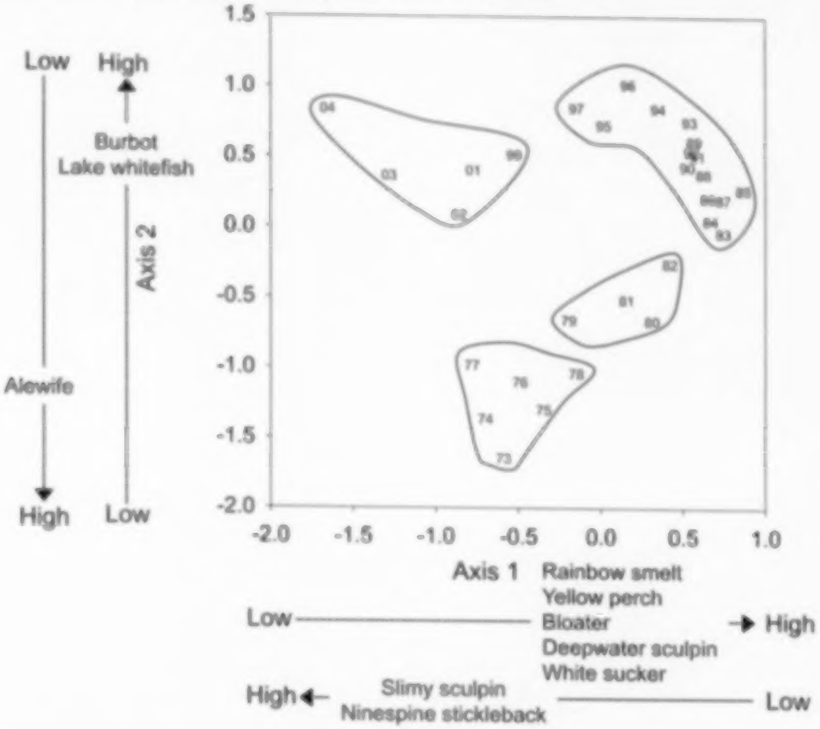
The impact of alewife biomass reductions on fish community changes

The impact of exotic alewives on native fish species in the Laurentian Great Lakes has been frequently reported and studied since the early 1970s (Smith 1970; Wells and McLain 1973; Crowder 1980). Alewife adults can negatively affect the recruitment of native fish fauna through two primary mechanisms: by preying upon their larvae (Smith 1970; Wells and McLain 1973; Krueger et al. 1995) or by competing with their young of year for zooplankton (Wells and McLain 1973). The predation mechanism has received greater attention in the literature (Crowder 1980; Rice et al. 1987; Luecke et al. 1990), and we focus on predation as the means by which alewife either was suppressing or may be continuing to suppress the recovery of native species. Because adult alewives generally inhabit the water column rather than the benthic area, native fish species whose larvae occupy the pelagia are most susceptible to alewife predation (Crowder 1980). Within the water column, alewives have been documented to consume larval yellow perch (Brandt et al. 1987; Mason and Brandt 1996) and lake trout (Krueger et al. 1995) in Lake Ontario embayments and also numerous other larvae of fish species in inland lakes (Kohler and Ney 1980). In addition, laboratory experiments have revealed alewives to be generally unsuccessful in consuming eggs or larvae at or near the bottom (Janssen 1978; Luecke et al. 1990).

The results of the NMS multivariate and cluster analyses provide support for the hypothesis that an alewife biomass reduction during the 1970s enabled the recovery of several native fish species in the 1980s through 1990s. First, the two native species that were associated with high alewife densities during the 1970s, slimy sculpin and ninespine stickleback, have a reproductive life history that likely minimizes the negative effect of alewife predation. Both species build nests in which the males guard the eggs and larvae even after their first feeding (McKenzie and Keenleyside 1970; Scott and Crossman 1973). Second, all of the native species that recovered in the 1980s or 1990s (during the time of lower alewife densities) have pelagic, unguarded larvae by the time of first feeding: bloater, burbot, deepwater sculpin, lake whitefish, white sucker, and yellow perch.

Although our correlative analyses suggest that the recovery of these native species is the result of the alewife reduction, our literature survey revealed that only the recoveries of burbot, deepwater sculpin, and yellow perch should be either partially or fully attributed to the reduction in alewife. Although no quantitative study in Lake Michigan exists,

Fig. 4. Nonmetric multidimensional scaling (NMS) ordination of annual biomass density species composition data collected from the US Geological Survey Great Lakes Science Center Lake Michigan bottom trawl survey. Numbers indicate the last two digits of the sampling year. Polygons encircle the groups of years identified to be similar using cluster analysis with a Sørensen's distance matrix and flexible beta linkage (also known as flexible clustering) where $\beta = -0.25$. Species names associated with each axis indicates the direction of the correlation between species biomass density and axis scores ($\alpha = 0.0025$).



Eshenroder and Burnham-Curtis (1999) stated that burbot restoration required the control of both parasitic-phase sea lampreys, which induce burbot mortality through attachment and feeding (Swink 2003), and a reduction in alewives. Effective sea lamprey control through the application of lampricide in Lake Michigan tributaries commenced in 1960 and enabled an 85% reduction of parasitic sea lampreys by 1966 (Lavis et al. 2003). Our time series, however, did not reveal a burbot recovery until the mid-1980s, which follows just after the considerable alewife reduction that had occurred by 1982. In our view, controlling both of these exotic species enabled the recovery of burbot observed in our bottom trawl survey during the 1980s and 1990s.

Previous studies have linked the recovery of deepwater sculpins and yellow perch to the decline in alewife biomass. During the 1970s and 1980s, deepwater sculpins were hypothesized to be negatively affected by predation from alewife and burbot (Smith 1970; Wells and McLain 1973; Madenjian et al. 2002), as well as by interspecific competition with slimy sculpin (Brandt 1986). Based on regression analyses, a recent study using the GLSC bottom trawl survey provided evidence that high densities of alewife and burbot did indeed reduce deepwater sculpin abundance, but there was no evidence that competition with slimy sculpin was an important factor (Madenjian et al. 2005*a*). Finally, previous studies concurred that the yellow perch recovery in the 1980s was facilitated by declines in alewife abundance (Wells 1977; Jude and Tesar 1985; Eck and Wells 1987). The yellow perch decline during the 1990s and 2000s, however, has been explained by several factors, including overfishing (Wilberg et al. 2005), low zooplankton densities (Dettmers et al. 2003), as well as continued alewife predation (Shroyer and McComish 2000).

For at least three other native species that recovered following the alewife decline, there is either limited or contradictory evidence to support a cause and effect relationship with alewife. First, bloater was commonly assumed to be negatively influenced by alewife densities during the 1970s and 1980s (Wells and McLain 1973; Eck and Wells 1987), likely because their dramatic recovery was observed soon after the alewife decline. A recently published study using the Lake Michigan GLSC bottom trawl survey, however, found no support for the hypothesis that bloater recruitment is limited by alewife densities (Bunnell et al. 2006). The model that best explained variation in bloater recruitment did not include adult alewife biomass, but did include adult bloater sex ratio and condition, as well as winter and spring temperatures (Bunnell et al. 2006).

With regard to lake whitefish, their recovery is believed to have been predicated upon the control of exotic sea lamprey in Lake Michigan (Eck and Wells 1987; Madenjian et al. 2002) and not on a reduction in alewife densities (Wells and

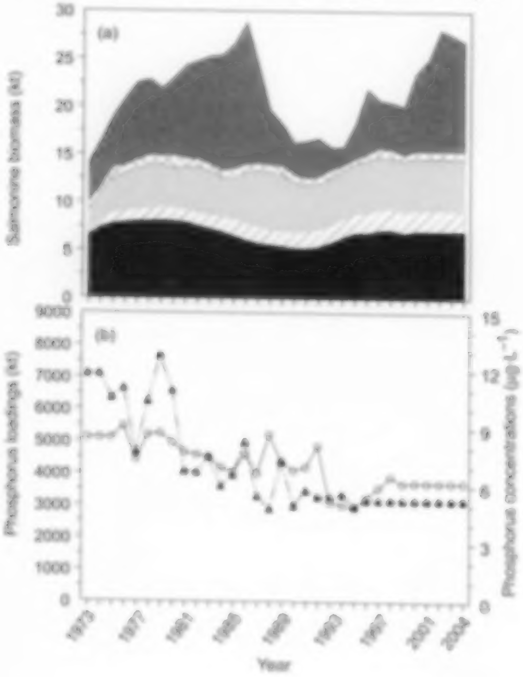


Fig. 5. Time series of estimated (*a*) salmonine biomass and (*b*) external phosphorus loadings (solid triangles and broken line on left *y* axis) and internal phosphorus concentrations (open circles and solid line on right *y* axis) in Lake Michigan. For (*a*), salmonine biomass equals the sum of lake trout (*Salvelinus namaycush*, solid area at bottom), brown trout (*Salmo trutta*, single hatched area), rainbow trout (*Oncorhynchus mykiss*, light gray area), coho salmon (*Oncorhynchus kisutch*, cross-hatched area), and Chinook salmon (*Oncorhynchus tshawytscha*, dark gray area at top).

McLain 1973). A time series of the commercial lake whitefish yields dating back to the 19th century reveals a decline in the late 1940s through the 1950s, which coincides with the period when parasitic-phase sea lamprey likely began targeting lake whitefish, because the preferred lake trout host had been nearly extirpated (Wells and McLain 1973). With the aforementioned 85% reduction of parasitic sea lampreys in the lake by 1966 (Lavis et al. 2003), lake whitefish yields began rising throughout the 1960s and have generally continued through the 2000s (Baldwin et al. 2002). Hence, this commercial time series reveals that the lake whitefish recovery began during a period when alewives were still extremely abundant. This response differs from that of the burbot population, which appeared to require reductions in both sea lamprey and alewife to recover (Eshenroder and Burnham-Curtis 1999).

White sucker is the final native species to have demonstrated a recovery following the reduction in alewives. Unfortunately, however, we know of no published studies on white sucker population dynamics in the Great Lakes and can offer little speculation as to the role of alewife. It is interesting, however, to note the absence of white suckers in our bottom trawl since 2001. Alewife biomass remained relatively unchanged over the entire period of modest increases in white sucker catches in the 1980s and early 1990s and then their nadir in the late 1990s.

The impact of other perturbations on fish community changes

In addition to the reduction of alewives, several other perturbations were occurring in Lake Michigan between 1973 and 2004 that could have been influencing fish community composition, including reductions in lake productivity, the introduction of dreissenid mussels, and changes in the biomass of salmonine predators. For two of these perturbations, lake productivity and salmonine biomass, we explored their effects on the fish community by correlating their time series with the axis scores of the fish community ordination. For dreissenid mussels, we have no time series of abundance with which to use in a correlation but do speculate on the timing of their introduction within the context of the ongoing fish community changes.

Since the implementation of the binational Great Lakes Water Quality Act in 1972, external total phosphorus loadings in Lake Michigan have declined; relative to the first estimate of loadings in 1974, loadings decreased by 43% by 1981 and by 58% by 1990, before leveling off between 1990 and 1995 (Madenjian et al. 2002). Declines in estimated phosphorus concentrations in the lake (average of nearshore and offshore sites) were less dramatic and were driven largely by interpolated declines in nearshore spring total phosphorus concentrations. Measurements of offshore total phosphorus concentrations have either decreased slightly from 1983 through 2000 (Barbiero et al. 2002) or demonstrated no trend between 1976 and 1998 (Madenjian et al. 2002). At nearshore sites, where we would predict declines in external loadings to have their greatest effects on total phosphorus concentrations, we know of only one nearshore total phosphorus time series, and it is limited to a few measurements in the mid-1970s and then additional measurements in the late 1990s, which revealed a 46% decline over those 20 or so years.

Both measures of lake productivity (i.e., external loading or internal concentrations of total phosphorus) were correlated with axis 2 of the NMS ordination, which suggests that the shift in fish community clusters including 1973–1982 to the clusters including 1983–2004 was related to reductions in lake productivity. In addition, these measures of lake productivity load on axis 2 in the same direction as alewife densities (high phosphorus through 1982, then lower through 2004). With regard to the effects of a phosphorus reduction on the fish community ordination, we view this correlation as largely spurious. First, Madenjian et al. (2005*b*) included this same phosphorus concentration time series in a regression analysis to explain alewife recruitment between 1962 and 2002, and phosphorus concentrations failed to explain recruitment variation. Hence, any argument supposing that oligotrophication has indirectly influenced the fish community by negatively influencing alewife biomass is unsubstantiated.

Second, we consider the possibility that the native fish species that recovered in the 1980s through 2000s benefited from this nutrient reduction. In central Lake Erie, a multivariate analysis of the fish community correlated declines in total phosphorus loadings and concentrations between 1969 and 1996 with increases in fish species richness (Ludsin et al.

2001). The presumed mechanism for this positive effect was the reduction in bottom anoxia, which resulted from lower nutrient loads. In Lake Michigan, however, this mechanism is unsupported because bottom anoxia has never been an issue in Lake Michigan proper. Hence, we know of no mechanism by which a reduction in nutrient concentrations would have promoted a recovery of the native fishes that we observed. Conversely, we cannot rule out the possibility that the reduction in nutrients contributed to the decline in species richness that we have observed since 2000. In western Lake Erie, Ludsin et al. (2001) found species richness to decline with oligotrophication (opposite from the central basin), because species that were generally tolerant of high nutrient environments (e.g., brown bullhead (*Ameiurus nebulosus*), common carp, channel catfish, goldfish (*Carassius auratus*), white crappie (*Pomoxis annularis*)) declined in abundance. Similarly, our richness declined because of absence of channel catfish, common carp, gizzard shad, freshwater drum, and white sucker, all of which can be considered tolerant of eutrophic conditions (Scott and Crossman 1973; Minns et al. 1994; Ludsin et al. 2001). It should be noted, however, that all of these species except white sucker have never been a major component of our samples, perhaps because our most shallow depth station was 9 m. When they were collected in our trawls, their numbers were typically rather low in number (channel catfish: mean = 2.1, range = 1–14; common carp: mean = 2.4, range = 1–11; gizzard shad: mean = 5.3, range = 1–45; freshwater drum: mean = 2, range = 1–6). In addition, we point out the inadequacy of the largely incomplete Lake Michigan nearshore productivity time series, which we assumed to be constant from 2001 through 2004. A more robust examination of whether the decline of these species is attributable to a decline in phosphorus concentrations would include measurements of nutrient concentrations in this nearshore habitat over this time period.

Correlations between salmonine biomass and the ordination axis scores were not significant, which implies that the fish community changes that we observed were not directly related to changes in salmonine biomass over the time series. In our view, however, salmonines have had at least an indirect effect on the native fish community through their consumption and top-down control of exotic alewives, which in turn, we have previously argued, contributed to the recovery of several of the native species during the 1980s and 1990s. Madenjian et al. (2005*b*) found strong evidence for salmonines to have limited alewife recruitment between 1962 and 2002, as alewives have always been a large majority of the salmonine total annual consumption (Madenjian et al. 2002). Given their high biomass levels and their critical role as the top predator in Lake Michigan, we presume that salmonines have had other effects on the native fish community, but additional research will be required to tease out those effects.

Finally, we consider the effect of the invasion of the zebra mussel in the late 1980s, as well as the invasion of its congener, the quagga mussel, in the late 1990s (Nalepa et al. 2001) on the Lake Michigan fish community. Dreissenids have been documented to influence several different trophic levels within the Laurentian Great Lakes (e.g., nutrients, Arnott and Vanni 1996; phytoplankton, Madenjian 1995; benthic macroinvertebrates, Nalepa et al. 1998). They are hypothesized to serve as a sink for nutrients that may have otherwise been transported farther offshore (Hecky et al. 2004), which in turn may limit abundance and production of offshore fish species while enhancing abundance and production of nearshore fish species (sensu Strayer et al. 2004). We could not evaluate the potential effect of dreissenids on our fish community ordination because no time series of dreissenid densities in Lake Michigan exists. Assuming that dreissenids became sufficiently abundant by the late 1990s, however, it remains a possibility that the shift in community composition and declines in fish biomass and species richness that occurred in the early 2000s also could be attributed to dreissenids. There is little evidence to support this hypothesis, however. In fact, opposite to the results of Strayer et al. (2004) in the Hudson River Estuary, we observed declines in biomass of nearshore (as well as intermediate and offshore) fishes during the 2000s, when dreissenids were presumably sequestering nutrients in the nearshore waters. In addition, the decline in species richness was a result of the absence of nearshore fish species captured during the survey. Hence, although changes in fish biomass, richness, and composition coincide with the likely increases in dreissenid abundance, the mechanism by which dreissenids could be driving these changes is not clear.

Some native species have yet to recover

Despite the recovery of several native species in Lake Michigan following the control of the exotic alewife population, several other species that were once present prior to 1973 (i.e., before our lake-wide bottom trawl survey began) have failed to return in sufficient numbers to be sampled in our survey. For example, we have never collected emerald shiners, although they have been sampled in various nearshore surveys during the 1970s through 2000s (see Madenjian et al. 2002). Prior to the 1960s, however, emerald shiners were so abundant that they supported a commercial fishery for a bait market, and they would occasionally block water intake screens (Flittner 1964). Because their dramatic decline in the 1960s coincided with the dramatic increase of alewife, conventional wisdom is that either alewife competition for zooplankton or alewife predation on emerald shiner eggs and larvae was responsible for the demise of emerald shiner (Smith 1970; Wells and McLain 1973). Because emerald shiners have not demonstrated a recovery in Lake Michigan, it appears that a 90% reduction in alewife biomass from the 1960s remains insufficient for an emerald shiner recovery.

Similar to emerald shiners, cisco was once so abundant in Lake Michigan that they supported a commercial fishery (Wells and McLain 1973). By 1955, however, commercial production underwent a precipitous decline and remained at unsubstantial levels during the 1960s. Today, a remnant Lake Michigan population is believed to exist only in Grand Traverse and Little Traverse Bay (Madenjian et al. 2002; Fitzsimons and O'Gorman 2006). Several factors likely caused the near extirpation of cisco in Lake Michigan, including overfishing, the negative effects of rainbow smelt and alewife, and perhaps habitat degradation (Wells and McLain 1973; Fitzsimons and O'Gorman 2006). Among the effect of exotic species, rainbow smelt are a more likely predator on cisco larvae than are alewife, given the greater temporal overlap during the period of cisco hatching (Christie 1974; Crowder 1980). Nonetheless, it remains unknown as to whether further reductions in alewife biomass would contribute to any cisco recovery in Lake Michigan.

Finally, lake trout rehabilitation has been stalled by the absence of natural reproduction in Lake Michigan, despite an annual stocking program since 1965 (Holey et al. 1995; Madenjian and Desorcie 1999). Our bottom trawl survey supported this contention by revealing only 1% of lake trout sampled to be unclipped, which is far less than the 5% expected frequency of unclipped, stocked lake trout (Madenjian et al. 2004). Several impediments to lake trout natural reproduction and rehabilitation have been hypothesized, including thiamine deficiency in lake trout eggs and resultant early mortality through consumption of alewife (Honeyfield et al. 2005), egg predation by numerous benthic invertebrate and fish species (Claramunt et al. 2005), or alewife predation on lake trout larvae (Krueger et al. 1995). Because alewife can hinder natural reproduction both through effects on lake trout egg quality and predation on lake trout larvae, it is possible that the alewife control that was achieved by 1982 remains insufficient to permit the natural reproduction and restoration of lake trout.

Management implications

The results of this study have implications for fishery managers on Lake Michigan and throughout the Great Lakes. First, managers can be gratified that their use of salmonines as a biological control appeared to have at least partially met its objectives by controlling the alewife population and establishing a recreational fishery for salmonines; lake trout recovery, however, has not occurred. At first glance, one might suppose that the alewife reduction also paved the way for the recovery of several ecologically (i.e., burbot, deepwater sculpin, white sucker) and commercially and recreationally (i.e., bloater, lake whitefish, yellow perch) important native species. We argue, however, that the alewife control had its greatest effect on burbot, deepwater sculpins, and yellow perch and that the resurgence of bloaters and lake whitefish may have been a spurious correlation with the alewife reduction. In addition, we noted that there are other native species that failed to demonstrate a recovery through our survey, including emerald shiner, cisco, and lake trout. Evidence from the literature suggests that alewives may have to be reduced to even lower levels for emerald shiners or lake trout to stage a recovery. Finally, managers should note the 1999–2004 shift in fish community composition that has coincided with a reduction in species richness and total fish biomass captured in our bottom trawl. In our view, other ongoing perturbations in Lake Michigan, such as nutrient reduction and establishment (and potential expansion) of dreissenid mussels, are not wholly sufficient to explain the fish community changes that we observed. We do, however, encourage more frequent monitoring of these two potentially important sources of fish community change than has been occurring. Hence, despite our ability to quantify and explain some of the effects of the exotic alewife on the native fish community, additional questions remain as ecologists and managers attempt to understand this dynamic and complex ecosystem.

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Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes

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Abstract: The effects of water color on lake stratification, mean epilimnetic irradiance, and lake temperature dynamics were examined in small, north-temperate lakes that differed widely in water color (1.5–19.8 m^{-1}). Among these lakes, colored lakes differed from clear lakes in the following ways: (*i*) the epilimnia were shallower and colder, and mean epilimnetic irradiance was reduced; (*ii*) the diel temperature cycles were more pronounced; (*iii*) whole-lake heat accumulation during stratification was reduced. The depth of the epilimnion ranged from 2.5 m in the clearest lake to 0.75 m in the most colored lake, and 91% of the variation in epilimnetic depth was explained by water color. Summer mean morning epilimnetic temperature was ~2 °C cooler in the most colored lake compared with the clearest lake. In clear lakes, the diel temperature range (1.4 ± 0.7 °C) was significantly ($p = 0.01$) less than that in the most colored lake (2.1 ± 1.0 °C). Change in whole-lake heat content was negatively correlated with water color. Increasing water color decreased light penetration more than thermocline depth, leading to reduced mean epilimnetic irradiance in the colored lakes. Thus, in these small lakes, water color significantly affected temperature, thermocline depth, and light climate.

Résumé : Les effets de la couleur de l'eau sur la stratification lacustre, l'irradiation moyenne de l'épilimnion et la dynamique de la température ont pu être examinés dans de petits lacs tempérés boréaux qui diffèrent considérablement de couleur (1,5–19,8 m^{-1}). Parmi les lacs, les lacs colorés se distinguent des lacs clairs par les caractéristiques suivantes : (*i*) leur épilimnion est moins profond et plus froid et leur irradiation épilimnique moyenne est réduite, (*ii*) les cycles journaliers de température sont plus prononcés et (*iii*) l'accumulation de chaleur dans le lac entier durant la stratification est réduite. La profondeur de l'épilimnion varie de 2,5 m dans le lac le plus clair à 0,75 m dans le lac le plus coloré; la couleur de l'eau explique 91 % de la variation de la profondeur de l'épilimnion. La température moyenne de l'épilimnion durant les matins d'été est de ~2 °C plus froide dans le lac le plus coloré que dans le lac le plus clair. Dans les lacs clairs, l'étendue journalière de la température (1,4 ± 0,7 °C) est significativement ($p = 0{,}01$) plus faible que dans le lac le plus coloré (2,1 ± 1,0 °C). Il existe une corrélation négative entre le changement de contenu calorique du lac entier et la couleur de l'eau. Une augmentation de la couleur de l'eau diminue plus la pénétration de la lumière que la profondeur de la thermocline, ce qui a pour effet de réduire l'irradiation moyenne de l'épilimnion dans les lacs colorés. Ainsi, dans ces petits lacs, la couleur de l'eau affecte de façon significative la température, la profondeur de la thermocline et le climat lumineux.

[Traduit par la Rédaction]

Introduction

Within lakes, physical characteristics such as water temperature, the depth of the epilimnion, and mean epilimnetic irradiance influence biological, chemical, and physical processes. The depth of the epilimnion determines the volume of water with favorable conditions for primary production (Arvola 1984) and affects the recycling of nutrients (Fee 1979). Epilimnetic depth and temperature determine the distribution of optimal habitat for warm, cool, or coldwater fishes (Stefan et al. 1996). Mixing depth also affects mean epilimnetic irradiance and determines the primary limiting factors (e.g., light, nutrients, or sinking rate) for algal production (Diehl 2002; Diehl et al. 2002; Ptacnik et al. 2003). Mean epilimnetic irradiance can affect algal succession, species composition, and algal production (Ramberg 1979; Fee et al. 1992). These physical lake characteristics are affected by lake morphometry (Hanna 1990; Sterner 1990; Fee et al. 1996), but may also be affected by in-lake characteristics such as water color.

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Table 1. Lake morphometry and related characteristics.

Lake	Area (ha)	Volume (m^3)	Area/volume	Maximum depth (m)	Mean depth (m)	Maximum fetch (m)	Depth of wave mixing (m)	Depth of epilimnion (m)*
Hummingbird	0.76	28 081	0.27	7.5	3.7	155	0.14	0.6 (0.1)
East Long	2.31	125 347	0.18	16.0	5.4	280	0.20	1.0 (0.1)
West Long	3.40	201 560	0.17	17.0	4.7	270	0.21	1.7 (0.2)
Tuesday	0.79	60 674	0.15	18.0	6.9	120	0.13	1.5 (0.1)
Paul	1.74	65 153	0.27	12.0	3.7	175	0.16	1.8 (0.2)
Peter	2.65	151 339	0.18	19.0	5.7	220	0.18	2.1 (0.2)

*Depth of epilimnion is 1999 mean (standard error in parentheses).

Table 2. Mean (standard error) summer 1999 limnological characteristics of study lake epilimnia.

Lake	Chlorophyll ($\mu g \cdot L^{-1}$)	Water color (a_{440} (m^{-1}))	DOC ($mg \cdot L^{-1}$)*	Total phosphorus ($\mu g \cdot L^{-1}$)	Total nitrogen ($\mu g \cdot L^{-1}$)	Secchi disk depth (m)
Hummingbird	32.0 (4.9)	19.8 (0.8)	22.0 (0.6)	38.8 (4.8)	1036.7 (102.2)	0.8 (0.05)
East Long	24.7 (3.2)	11.0 (0.2)	12.4 (0.3)	42.1 (6.25)	813.9 (35.0)	1.1 (0.04)
West Long	10.2 (1.0)	4.4 (0.12)	8.5 (0.2)	23.7 (4.3)	605.9 (48.1)	2.2 (0.07)
Tuesday	7.3 (0.7)	3.5 (0.1)	7.9 (0.1)	11.9 (0.9)	485.4 (40.8)	2.4 (0.08)
Paul	3.2 (0.3)	1.5 (0.05)	4.3 (0.05)	11.0 (0.7)	371.2 (13.8)	4.8 (0.1)
Peter	8.4 (0.6)	1.5 (0.04)	5.1 (0.14)	13.2 (1.6)	570.6 (12.9)	3.3 (0.1)

*Dissolved organic carbon.

In lakes of low to moderate productivity, water color is derived primarily from dissolved organic carbon (DOC) of terrestrial origin (Jones and Arvola 1984; Kirk 1994; Fee et al. 1996). Colored DOC inputs to lakes are highly variable in space and time. Among-lake variability is generally explained by watershed characteristics (Engstrom 1987; Kortelainen 1993; Dillon and Molot 1997), and temporal variability is driven by climatic factors (e.g., rainfall; Schindler et al. 1997; Pace and Cole 2002). Thus, water color derived from terrestrial DOC is an important link among lakes, their watersheds, and climate and may be important in mediating the response of physical lake characteristics to changes in climate (Magnuson et al. 1997; Schindler et al. 1997).

A direct effect of high water color in lakes is rapid light attenuation with depth. As a result, in high color lakes the warming effect of solar radiation is restricted to shallower depths than in low color lakes. In small lakes, increased light attenuation by water color is correlated with decreased depth of the epilimnion (Kling 1988; Mazumder and Taylor 1994; Fee et al. 1996). If the reduction in thermocline depth with increased water color exactly compensates for increased light attenuation, the irradiance at the thermocline, and therefore mean epilimnetic irradiance, remains constant. Thus, the net effect of increases in water color on mean epilimnetic irradiance in small lakes depends on the relationship between the magnitude of the effect of water color on epilimnetic depth and the magnitude of the effect of water color on light attenuation.

The effects of water color on light penetration and thermocline depth provide mechanisms through which water color may affect the temperature dynamics of lakes. Colored lakes experience reduced heating of hypolimnetic waters (Bukaveckas and Driscoll 1991; Snucins and Gunn 2000; Dillon et al. 2003), most likely because of decreased penetration of solar irradiance. Similarly, Bowling (1990) suggested that colored lakes might have relatively low heat content. A shallower epilimnion results in a higher surface area to volume ratio, which may cause more pronounced diel epilimnetic temperature fluctuations. There is anecdotal evidence that water color affects epilimnetic temperature dynamics fluctuations (Bowling and Salonen 1990), but there have been no direct comparisons of surface temperatures and diel temperature dynamics among nearby lakes of similar size and morphology that differ substantially in water color.

Water color is highly variable among lakes in north-temperate regions, with neighboring lakes of similar morphometry exhibiting large differences in water color (Pace and Cole 2002). Understanding how physical and chemical processes differ among these lakes requires understanding the effects of water color on these processes. Here, I focus on the effects of water color on thermocline depth, mean epilimnetic irradiance, and water temperature in small, north-temperate lakes. Although a number of the relationships among water color, irradiance, and lake thermal characteristics are known (e.g., Kling 1988; Fee et al. 1996; Snucins and Gunn 2000), important questions remain, and two of these are addressed in this paper. (*i*) What is the effect of water color on mean epilimnetic irradiance? (*ii*) How does water color affect epilimnetic temperature dynamics and whole-lake heat content?

Materials and methods

Study site and sampling program

This study included six small, north-temperate lakes (Hummingbird, East Long, West Long, Tuesday, Paul, and Peter lakes) that were of similar size and morphometry, were located within a few kilometres of each other, and spanned a wide range of DOC concentrations and water color (Tables 1 and 2). The lakes are located on the University of Notre Dame Environmental Research Center property near Land o' Lakes, Wisconsin, USA. These lakes are deep relative to their surface area and have a hyperboloid geometry that is often observed in kettle lakes (Carpenter 1983). The upland forests around the lakes are dominated by sugar maples (*Acer saccharum*) along with red maple (*Acer rubrum*), yellow birch (*Betula lutea*), eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), and white spruce (*Picea glauca*). The lakes are generally surrounded by *sphagnum* bogs containing black spruce (*Picea mariana*), eastern white-cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), bog rosemary (*Andromeda polifolia*), and labrador tea (*Ledum groenlandicum*). A more detailed description of this region and its lakes can be found in Carpenter and Kitchell (1993).

Three of the lakes (Peter, East Long, and West Long lakes) were experimentally fertilized with phosphorus (P) and nitrogen (N) from 1993 to 1997 as part of a set of whole-lake experiments designed to determine the effect of food-web structure, nutrient inputs, and DOC concentrations on primary production (Carpenter et al. 2001). P fertilization rates per lake surface area ranged from approximately 1 to 6 $\mathrm{mg \cdot m^{-2} \cdot day^{-1}}$ (N/P in the fertilizer exceeded 30 (by atoms) to prevent N limitation).

The study lakes were sampled weekly during the summer stratified period (mid-May to early September). Four of the lakes (Peter, Paul, East Long, and West Long lakes) were sampled during 1991–1999, and two of the lakes (Hummingbird and Tuesday lakes) were sampled only during the 1999 field season. The effects of water color and chlorophyll on depth of the epilimnion and mean epilimnetic irradiance were examined using data from 1991 to 1999. The effects of water color on epilimnetic temperature dynamics and whole-lake heat content were investigated using the six-lake 1999 data set.

Limnological methods

Epilimnetic water color samples were collected by pooling mixed layer water from multiple depths (0, 1, and 2 m in Peter, Paul, Tuesday, and West Long lakes; 0, 0.5, and 1 m in East Long Lake; 0.5 m in Hummingbird Lake), filtered (GF/F), and analyzed spectrophotometrically in a 10 cm cuvette. Color was expressed as a wavelength-specific (440 nm) absorption coefficient (units are inverse metres, $\mathrm{m^{-1}}$): $a_{440} = 2.303 \times$ (absorbance at 440 nm/0.1 m). This absorption coefficient serves as a relative measure of the brown color of lake water by indicating the content of light-absorbing (primarily humic) materials in the water (Pace and Cole 2002). Integrated epilimnetic chlorophyll was determined as the volume-weighted mean of chlorophyll concentrations at three depths: surface, the depth of 50% surface irradiance, and the depth of 25% surface irradiance. Chlorophyll *a* was collected on GF/F filters and extracted overnight in 25 mL of 100% methanol. Chlorophyll *a* concentrations in the extracted sample was quantified fluorometrically using a Turner 450 fluorometer equipped a quartz–halogen lamp, SC665 emission filter, and NB440 excitation filter and corrected for pheopigments (Marker et al. 1980).

Irradiance in the photosynthetically active waveband of 400–700 nm was measured just below the lake surface, every 0.25 m for the first metre, and every 0.5 m thereafter until the depth of 1% surface light was reached using a LI-COR spherical quantum sensor (LI-193SB). Temperature profiles were measured using a YSI temperature – dissolved oxygen meter. In 1999, temperature profile sampling began at approximately 0845 ± 15 min for Paul, West Long, and Tuesday lakes and at 0945 ± 15 min for Peter, East Long, and Hummingbird lakes. Measurements were taken at 0.5 m intervals from the surface through the metalimnion, then at 1 m intervals in the hypolimnion. The bottom of the epilimnion was defined graphically after Wetzel (2001). The temperature profile was divided into the homoiothermal surface layer and the metalimnion characterized by a steep temperature gradient. Straight lines were fit by eye to each of these regions of data, and their intersection defined the depth of the epilimnion. The depth of wave mixing was calculated based on maximum lake fetch and an assumed wind speed of 1.5 $\mathrm{m \cdot s^{-1}}$ using the equations of Smith and Sinclair (1972).

In 1999, diel temperature cycles were measured in Peter and Paul lakes (clear lakes) and East Long Lake (colored lake) using Endeco-YSI sondes (model UPG-6000), which recorded epilimnetic temperature every 5 min. Owing to logistical constraints, one sonde was deployed in East Long Lake while a second sonde was deployed alternatively in Peter and Paul lakes. Data was collected simultaneously from East Long and Peter or Paul lakes on 24 days between 24 May and 24 August. Sampling was approximately biweekly in late May – early July, weekly during July, and biweekly in August. The sondes were deployed at 0.7 m (Peter and Paul lakes) or 0.5 m (East Long Lake) near the center of the lake. Because the high color lake and clear lakes were measured with separate sondes, the sonde measurements were compared with simultaneous measurements made with the YSI temperature probe as part of the weekly temperature profiles. The sondes and the YSI temperature probe agreed well, and no systematic difference between sondes was discernible (Houser 2001). For example, the average difference between the temperatures measured by the YSI and the sondes in the colored and clear lakes was –0.08 and –0.1 °C, respectively. Differences of this magnitude are too small to substantially affect our conclusions. For clarity, in the Results and Discussion sections pertaining to the sonde data, East Long Lake (a high color lake) is referred to as the "colored" lake, whereas Peter and Paul (low color lakes) are referred to as "clear" lakes.

Lake morphometry

The bathymetric data were collected by running constant-speed transects between shore and midlake landmarks. The positions of shore and midlake landmarks were triangulated using a KVH Datascope™ flux-gate compass. Depth data were collected at 1 $\mathrm{s^{-1}}$ using the data stream from a discriminating digital sonar logged on a laptop computer. Between 4000 and 8000 sets of depth, latitude, and longitude coordinates were collected in each lake. The data were reduced to a contour grid by ordinary kriging (no drift was allowed and no anisotropy specified). The resulting grids were plotted as simple morphometric maps and analyzed to determine areas and volumes of strata.

Mean epilimnetic irradiance

Riley (1957) developed an expression for mean mixed layer irradiance, which was modified by Sterner (1990) to express mean epilimnetic irradiance as a proportion of the surface irradiance:

$$(1) \qquad \bar{E}\% = \frac{100(1 - e^{-kZ_T})}{kZ_T}$$

where $\bar{E}\%$ is the mean epilimnetic irradiance as a percentage of the surface irradiance, k is the diffuse attenuation coefficient for irradiance in the photosynthetically active waveband, and Z_T is the depth of the thermocline. k was calculated for each sampling day as the slope of a linear regression of log-transformed irradiance versus depth and then used in eq. 1 to calculate mean epilimnetic irradiance.

Heat content

The heat content of the lakes (Θ_w) was calculated weekly for each lake in 1999 as follows (Johnson et al. 1985):

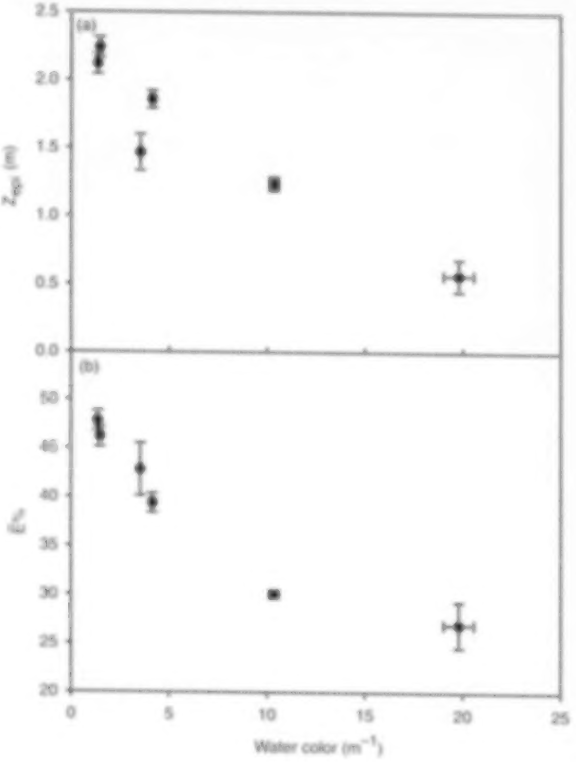
$$(2) \qquad \Theta_w = A_0^{-1} \sum_{z_0}^{z_{max}} C_p T_z A_z h_z$$

where C_p is the specific heat of water (cal·m^{-3}·°C^{-1}; 1 cal = 4.186 J), A_0 is the surface area of the lake (m^2), z_0 is the lake surface (z = 0 m), z_{max} is the maximum depth (m), T_z is the temperature at depth z (°C), A_z is the area at depth z (m^2), and h_z is the thickness of the layer of water centered at depth z (m). For comparison among lakes, the change in heat content (S) was calculated as the difference between the heat content (Θ_w) the week of 25 May and the week of 28 July when maximum heat content was observed in most of the lakes.

Data analysis

Multiple regression analysis was used to test for significant (p = 0.05) relationships between predictor and response variables. The response variables included depth of the epilimnion (Z_{epi}), mean epilimnetic irradiance ($\bar{E}\%$), epilimnetic temperature (T_{epi}), and whole-lake heat accumulation (S). The following predictor variables were included in the analysis: water color, chlorophyll, lake surface area, surface area/volume, maximum fetch, and maximum depth. Water color and chlorophyll were log-normally distributed and were log-transformed for regression analysis. Linear regression analysis was performed for each of the response variables in SAS (Release 8.02, SAS Institute Inc., Cary, North Carolina), and variables were chosen for inclusion in the model using a stepwise procedure that selected independent variables based on the F statistic associated with each variable. This procedure never selected more than two significant variables for inclusion in the model. Because of the small data set and the distribution of the lakes across a water color gradient, we conducted an influence analysis for each of these regressions using the DFBETAS influence diagnostic recommended by Belsley et al. (1980, as cited in SAS Institute Inc. 2004).

Fig. 1. Relationship between water color and (*a*) mean depth of the epilimnion (Z_{epi}) and (*b*) mean epilimnetic irradiance ($\bar{E}\%$). Error bars are one standard error. Regression results for log-transformed data are shown in Table 3.



Results

Depth of the epilimnion and mean epilimnetic irradiance

Water color strongly affected epilimnetic depth and mean epilimnetic irradiance. Epilimnetic depth ranged from 2.2 m in the clearest lake to 0.6 m in the most colored lake (Fig. 1*a*), and 91% of the variation in epilimnetic depth was explained by water color (Table 3; Fig. 1*a*). Lake surface area explained an additional 7% of the variability in the depth of the epilimnion and was only marginally significant (p = 0.06). The mean epilimnetic irradiance for each lake as a percentage of surface light ($\bar{E}\%$) ranged from ~50% in the clearest lake to ~25% in the most colored lake (Fig. 1*b*). Water color explained 97% of the variability in mean epilimnetic irradiance among lakes (Table 3). Summer mean chlorophyll concentration, surface area/volume, maximum fetch, and maximum depth did not explain significant variability in the depth of the epilimnion or mean epilimnetic irradiance.

Mean epilimnetic irradiance is a function of the light extinction coefficient (k) and the depth of the epilimnion (eq. 1). The average k for each lake was primarily determined by water color (k = 0.5 – 1.68 ln(water color); R^2 = 0.87, p <

Table 3. Results of multiple regression analysis of effects of water color and lake morphometry on depth of the epilimnion (Z_{epi}), mean epilimnetic irradiance ($\bar{E}\%$), average epilimnetic temperature (T_{epi}), and heat content (S).

Dependent variable	Slope	Independent variable	Partial R^2 (p)	Model R^2 (p)
Z_{epi}	−0.47	ln(water color)	0.91 (0.0024)	0.98 (0.003)
	0.14	Surface area	0.07 (0.059)	
$\bar{E}\%$	−8.1	ln(water color)	0.97 (0.006)	0.97 (0.0007)
T_{epi}	−0.64	ln(water color)	0.92 (—)	0.92 (0.002)
S	0.55	Maximum depth	0.81 (0.015)	0.97 (0.004)
	−1.72	ln(water color)	0.17 (0.021)	

Fig. 2. Weekly epilimnetic temperatures (standardized by subtracting the weekly mean temperature of all six lakes from each lake temperature) vs. water color. The data shown are the means and standard errors of weekly data from May to August 1999.

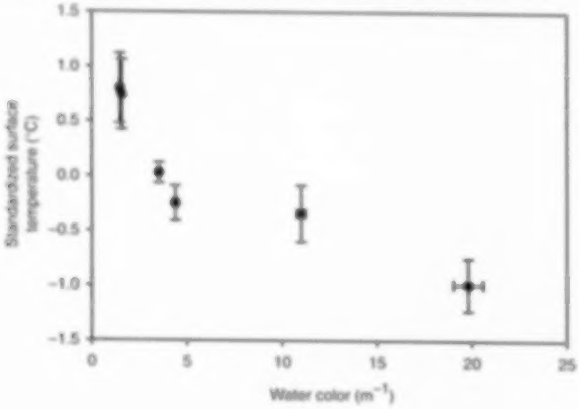
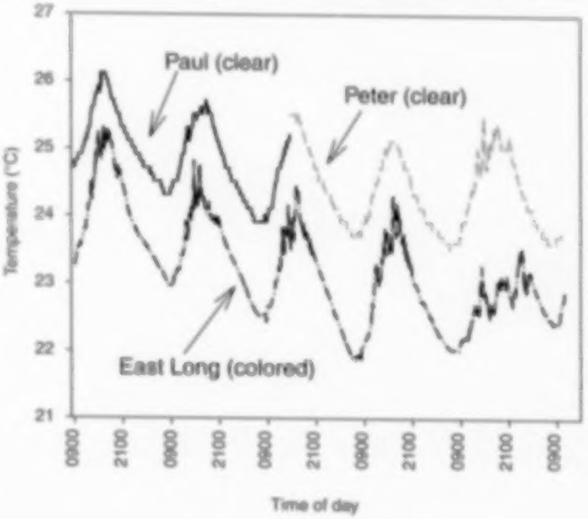


Fig. 3. Epilimnetic temperature cycles for Paul, Peter, and East Long lakes from 2 August through 7 August 1999. Upper line represents temperatures in Paul (solid line) and Peter lakes (dashed line), which are both clear lakes, for 2 days each. Lower dot-dashed line represents East Long Lake (colored lake) for the 4 consecutive days. Temperature was measured every 5 min.



0.01, $n = 6$). Values of k ranged from 0.3 m^{-1} in the clearest lake to 6.7 m^{-1} in the most colored lake. Thus, water color simultaneously reduced the irradiance at any given depth and the depth of the bottom of the epilimnion. The net effect of these processes was to reduce mean epilimnetic irradiance (Table 3; Fig. 1*b*), indicating that across the gradient of water color studied here, the depth of light penetration decreased more than the depth of the epilimnion.

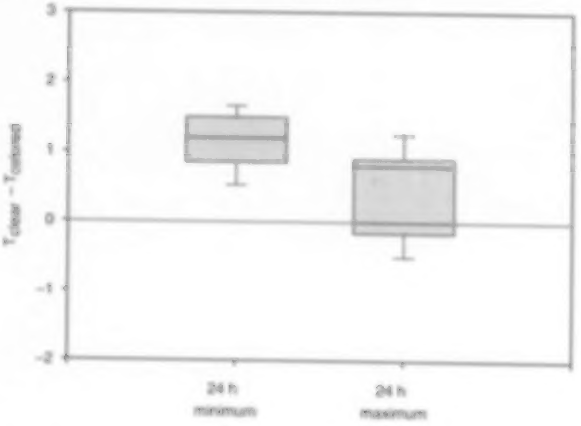
Epilimnetic temperature

Morning epilimnetic water temperature and the magnitude of epilimnetic diel temperature cycles were both significantly affected by water color. More colored lakes had significantly lower morning epilimnetic temperatures (Table 3). Summer mean morning epilimnetic temperature was ~2 °C cooler in the most colored lake compared with the clearest lake (Fig. 2). Epilimnetic temperatures measured midway between the surface and bottom of the epilimnion showed a diel temperature cycle, with minimum and maximum temperatures occurring at approximately 0900 and 1800, respectively (Fig. 3). In clear lakes (Peter and Paul lakes), the diel temperature range (mean (standard deviation) = 1.4 (0.7)) was significantly less than in the colored lake (East Long Lake, 2.1 (1.0); two sample t test, $t = 2.7$, $p = 0.01$). The daily minimum temperature was always cooler in the colored lake, and the difference ranged from 0.2 to 2.6 °C (mean = 1.17 °C) (Fig. 4). The daily maximum temperature was cooler in the colored lake 17 days out of 23, and the difference in maximum temperature ($T_{clear} - T_{color}$) ranged from 1.4 to −1.5 °C (mean = 0.5 °C) (Fig. 4). Thus, the colored lake showed cooler morning epilimnetic temperatures and a wider diel temperature range.

Whole-lake heat content

The change in whole-lake heat content ranged from a minimum of 13.8 W·m^{-2} in Hummingbird Lake (highly colored) to a maximum of 24.4 W·m^{-2} in Peter Lake (clear) and was negatively correlated with water color. Maximum lake depth explained much of the variation in whole-lake heat accumulation (81%), and water color explained most of the remaining variation (17%) (Fig. 5; Table 3). The model containing these two variables explained 97% of the variation in whole-lake heat accumulation. The reduced heat accumulation in the colored lakes is evident in the midsummer, morn-

Fig. 4. Boxplot of the differences between minimum and maximum epilimnetic temperatures each day in clear (Peter or Paul lakes) and colored (East Long Lake) lakes. The line inside the box represents the median, the upper and lower ends of the box represent the 25th and 75th percentiles, respectively, and the whiskers represent the 10th and 90th percentiles.



ing temperature profiles (Fig. 6), which showed that colored lakes were cooler than the clear lakes across all depths, and the depth at which the hypolimnetic minimum temperature was reached was shallower in more colored lakes.

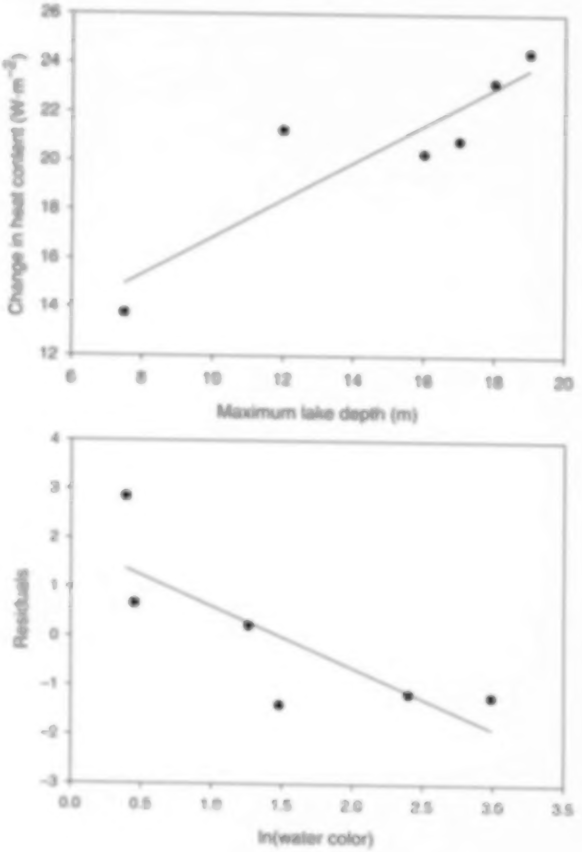
The results of the influence analysis did not suggest that any of the significant relationships identified above are due to the influence of a single lake and indicated only one instance of a strong influence of an individual data point. Paul Lake (a clear lake) was identified as having significant influence in the regression of Z_{epi} vs. lake surface area and water color. Removal of Paul Lake from the analysis improved the fit of the regression model somewhat and had no qualitative effect on the resulting conclusions.

Discussion

The results presented here synthesize the multiple physical effects that water color can exert on small lakes. Across the gradient of water color exhibited by these study lakes, the depth of light penetration decreased more than the depth of the epilimnion, resulting in reduced mean epilimnetic irradiance in the colored lakes. The lakes in the current study were small and characterized by minimal wind exposure. Thus, these lakes would be expected to exhibit the maximum effects of light attenuation on the depth of the epilimnion likely to occur in lakes (Fee et al. 1996). The results presented here show that in these small, wind-protected lakes, the reduction in thermocline depth with increased water color was insufficient to compensate for the reduced light penetration.

Theoretical and empirical work has shown that mean epilimnetic irradiance, a function of light extinction and mixing depth, can affect various aspects of phytoplankton dynamics and community structure, including species diversity, total density, total biomass, and production (Litchman 2000; Millard and Sager 1994; Diehl et al. 2002). There is evidence that differences in mean epilimnetic irradiance of the

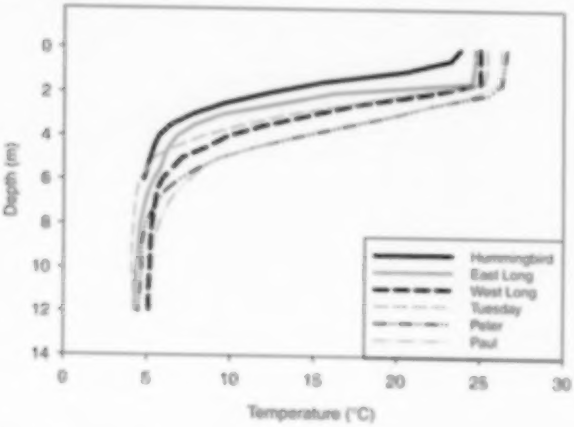
Fig. 5. The effects of maximum lake depth and water color on the change in whole-lake heat content between 25 May and 28 July 1999: (*a*) maximum lake depth vs. change in heat content and (*b*) the residuals of the regression of maximum lake depth vs. change in heat content and ln(water color). Solid lines are trend lines.



magnitude shown here can affect phytoplankton communities. For example, Diehl et al. (2002) found that across a mean epilimnetic irradiance gradient that ranged from 10% to 45% of surface irradiance, there was a strong correlation between mean epilimnetic irradiance and phytoplankton community production.

Detailed studies have shown that the relationship between phytoplankton production and irradiance is complex. The trajectories of individual algal cells within the epilimnion can be affected by complex mixing dynamics (MacIntyre 1993), and mean epilimnetic irradiance is only an approximate measure of the light environment experienced by mixed layer phytoplankton. Furthermore, during periods of high water column stability, motile phytoplankton (e.g., dinoflagellates) can migrate to depths of preferred irradiance (e.g., Heaney and Talling 1980). Thus, the light climate experienced by individual phytoplankton cells probably differs from the mean epilimnetic irradiance. Nonetheless, Klug and Cottingham (2001), in a detailed study of the algal communities of some of the lakes included in the current study,

Fig. 6. Midsummer temperature profiles for the six study lakes. The legend shows lakes in order of decreasing color concentration. Data shown are from 26 to 28 July 1999. Note that there was not a large difference in thermocline depth across the gradient in water color; differences in thermocline depth are better illustrated by summer means.



found that differences among the phytoplankton communities may be partially explained by the effects of colored DOC on the epilimnetic light environment.

The current study focused on lakes that differ strongly in water color and, to a lesser extent, in chlorophyll concentration and thereby highlights the effects on lakes of water color. Chlorophyll *a* concentration has been shown to affect mean epilimnetic irradiance and the depth of the epilimnion (e.g., Mazumder et al. 1990; Huisman and Weissing 1995), but was not a significant driver of mean epilimnetic irradiance or depth of the epilimnion in this study. The fact that chlorophyll *a* dynamics occur on relatively short time scales may cause the effects of chlorophyll concentration on lake characteristics to be obscured at the time scales examined here.

Increased water color was also associated with changes in lake temperature dynamics. In colored lakes, the morning epilimnetic temperatures were cooler and the diel temperature cycle spanned a wider range. These results may be partly explained by the shallower epilimnetic depth in the colored lakes. A lake with a shallower epilimnion has greater surface area per epilimnetic volume, facilitating heat loss from the epilimnion to the atmosphere during the cool evenings typical in this region. Furthermore, the reduced volume of the epilimnion in a colored lake, combined with the increased rate of light attenuation, results in more light energy being absorbed per volume in the colored lakes and should cause greater heating during the day. The effect of the higher rate of cooling and warming in the colored lakes can be seen in the fact that in 19 of 24 comparisons of 24 h temperature cycles between a clear and colored lake, the colored lake showed a larger temperature range. However, on only 6 of 24 days was the maximum epilimnetic temperature (measured mid-depth in the epilimnion) higher in the colored lake, indicating that the rate of heating during the day did not completely compensate for the higher rate of heat loss at night in the colored lakes.

Change in whole-lake heat content during stratification was lower in colored lakes. Solar radiation penetrated into the hypolimnion in the clear lakes, but little solar radiation reached below the thermocline in the small, colored lakes in this study (Houser et al. 2003). Heat absorbed by the hypolimnion is not directly available to exchange with the atmosphere. Thus, heat storage in the hypolimnion may increase the heat content of the clear lakes, whereas in a highly colored lake, little heat accumulates in the hypolimnion. Furthermore, the cooler morning epilimnetic temperatures and wider diel temperature range in the epilimnion of the colored lakes indicate that much of the heat absorbed in the epilimnion during the day in a colored lake is lost at night. These processes are reflected in midsummer temperature profiles from these lakes and whole-lake heat accumulation during the summer. The clear lakes show heating much deeper into the water column than do the colored lakes. As a result, the heat accumulation in the colored lakes is much reduced compared with that of the clear lakes. In summary, high color lakes appear to accumulate heat derived from solar irradiance in the epilimnion where it is readily returned to the atmosphere, whereas in clear lakes there is heat storage in the hypolimnion where it accumulates.

If the magnitude and temperature of groundwater inputs were sufficient to affect epilimnetic temperature, it is possible that groundwater had a larger effect on the colored lakes because of the smaller epilimnetic volume. Hydrologic tracer (LiBr) additions to Peter, East Long, and West Long lakes showed that groundwater inputs were low (0.48 ± 0.36 cm·day^{-1}; Cole and Pace 1998) and were not correlated with DOC or water color concentrations. To estimate the effects of groundwater input on epilimnetic water temperature, the following assumptions were made: (*i*) groundwater input rate to each lake was equal (on an areal basis) among lakes at 0.5 cm·day^{-1}; (*ii*) all groundwater inputs were to the epilimnion; (*iii*) groundwater temperature was 12 °C and epilimnetic temperature was 22 °C. Under these conditions, groundwater inputs would reduce epilimnetic temperatures over a 24 h period as follows: Hummingbird Lake, 0.09 °C; East Long Lake, 0.05 °C; West Long Lake, 0.03 °C; Tuesday Lake, 0.03 °C; Paul Lake, 0.02 °C; Peter Lake, 0.02 °C. Thus, the difference in groundwater influence on epilimnetic temperature between the most colored lake (Hummingbird Lake) and the clearest lake (Peter Lake) is trivial (0.07 °C) compared with the differences in epilimnetic temperature observed among lakes and consequently cannot explain the observed differences in epilimnetic temperatures.

The diel temperature data were collected with sondes deployed at a single depth in the epilimnion (0.7 m (clear lakes) and 0.5 m (colored lake)), and as a result these data do not reflect the complex mixing and stratification that can occur within the epilimnion (Imberger 1985). The epilimnion may stratify, forming a layer of warm water at the surface, particularly on calm, sunny days. If such stratification occurred, the data from the depth of sonde deployment do not reflect all of the temperature changes that occur within the epilimnion. However, morning temperature profiles (collected weekly) indicated that the differences between water at the sonde depth and at the surface were very small and of similar magnitude and distribution (mean temperature differences (°C) ± standard error: East = –0.16 ± 0.09, Paul =

–0.16 ± 0.09, Peter = –0.12 ± 0.09). In addition, tracer additions to these lakes have shown that the epilimnion is well mixed both horizontally and vertically on a daily basis (Cole and Pace 1998). This mixing, and the consistency and small magnitude of the differences between surface temperature and sonde measurements at midmorning, indicates that the differences among lakes observed in the sonde data reflect real differences in lake epilimnetic temperatures.

It does not appear that differences among the study lakes characteristics associated with size, such as increased influence of shading by trees or increased shelter from the wind, have confounded the results. If increased shading by surrounding trees, because of the greater ratio of lake shore to lake area in a smaller lake, caused cooler temperatures, Paul Lake (1.74 ha) should have had cooler epilimnetic temperatures than East Long (2.31 ha) or West Long lakes (3.40 ha) instead of the warmer epilimnetic temperatures that were observed. All of the study lakes are quite sheltered from the wind, and wave mixing occurs only to a shallow depth. Surface area was a marginally significant predictor of mixing depth, and it was clearly not the dominant factor. For example, East Long Lake had a shallower epilimnion than Paul or Peter lakes, despite the greater wind exposure and therefore greater estimated depths of wave mixing.

In the abundant small lakes of north-temperate regions, water color can affect a range of physical lake characteristics. In the group of small lakes studied here, colored lakes differed from clear lakes in the following ways: (*i*) the epilimnia were shallower and colder, and mean epilimnetic irradiance was reduced; (*ii*) the diel temperature cycles were more pronounced; (*iii*) whole-lake heat accumulation during stratification was reduced. Because water color in these lakes is largely derived from terrestrial, refractory DOC (Christensen et al. 1996, Houser et al. 2003), these results contribute to the growing evidence that terrestrial DOC input rate is a key variable in structuring lake ecosystems (e.g., Fee et al. 1996; Carpenter et al. 1998; Snucins and Gunn 2000) and should be considered when predicting changes that may occur in lakes in response to changing climatic conditions and patterns of land use.

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Hierarchical approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in southeastern Australia

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Abstract: A three-levelled hierarchical risk assessment approach was trialed using piked spurdog (*Squalus megalops*) to evaluate the suitability of the approach for chondrichthyan species. At level 1, a qualitative assessment indicated that the only fishing-related activity to have moderate or high impact on *S. megalops* was "capture fishing" by otter trawl, Danish seine, gillnet, and automatic longline methods. At level 2, a semi-quantitative assessment ranked *S. megalops* at risk because of its low biological productivity and, possibly, its catch susceptibility from cumulative effects across the separate fishing methods. Finally, at level 3, a quantitative assessment showed that population growth is slow even under the assumption of density-dependent compensation where the fishing mortality rate equals the natural mortality rate. Although published information indicates that relative abundance has been stable in several regions of southern Australia, it is concluded that given its low biological productivity, changed fishing practices leading to increased fishing mortality could quickly put *S. megalops* at high risk. The hierarchical approach appears particularly useful for assessment of chondrichthyan species in data-limited fisheries. This approach allows for a management response at any level, optimizing research and management efforts by identifying and excluding low-risk species from data intensive assessments.

Résumé : Nous employons une méthode hiérarchique à trois niveaux pour l'évaluation des risques chez le requin aiguillat (*Squalus megalops*) afin de vérifier si la méthode s'applique aux espèces de chondrichthyens. Au niveau 1, une évaluation qualitative indique que la seule activité de pêche qui ait un impact modéré ou élevé sur *S. megalops* est la « pêche de capture » faite par les méthodes du chalut à panneaux, de la seine danoise, du filet maillant et de la palangre automatique. Au niveau 2, une évaluation semi-quantitative considère *S. megalops* à risque à cause de sa faible productivité biologique et, peut-être, sa susceptibilité à la capture due aux effets cumulatifs des différentes techniques de pêche. Enfin, au niveau 3, une évaluation quantitative montre que la croissance de la population est lente, même si on assume une compensation dépendante de la densité dans laquelle le taux de mortalité due à la pêche est égal au taux de mortalité naturelle. Bien que les informations publiées indiquent que l'abondance relative de *S. megalops* est stable dans plusieurs régions du sud de l'Australie, nous concluons qu'à cause de sa faible productivité biologique, des changements dans les pratiques de pêche qui mèneraient à une mortalité accrue due à la pêche pourraient placer l'espèce dans une position de grand risque. La méthode hiérarchique semble particulièrement utile pour l'évaluation des espèces de chondrichtyens dans des pêches commerciales pauvres en données. Cette approche permet une réaction de gestion, à divers niveaux, et elle optimise les efforts de recherche et de gestion en identifiant et en excluant les espèces à faible risque des évaluations fondées sur des bases importantes de données.

[Traduit par la Rédaction]

Introduction

Globally, only limited attempts have been made to manage populations of chondrichthyan species impacted by the effects of fishing (Anderson 1990; Bonfil 1994). The few exceptions have focused on target species such as gummy shark (*Mustelus antarcticus*) (Walker 1998), school shark (*Galeorhinus galeus*) (Punt et al. 2000), and dusky shark (*Carcharhinus obscurus*) (Simpfendorfer 1999) in southern Australia. Although biological parameter estimates and time series of catch, fishing effort, and other monitoring data have been collected to enable stock assessment for sustainable use of the high-valued species, there is a paucity of such information for non-target species (Bonfil 2004). Given the comparatively low biological productivity and often high catch susceptibility of chondrichthyan species (Stobutzki et al. 2002; Walker 2004), management initiatives are needed long before sufficient data can be collected for stock assessment

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(Walker 2004). Concerns about widespread depletion of chondrichthyan populations led the United Nations Food and Agricultural Organization (FAO) to develop an International Plan of Action for the Conservation and Management of sharks (IPOA sharks) (FAO 2000) that was implemented during 1999.

More recently, to address the concerns of uncertainty associated with the wider impacts of fishing on marine ecosystems, Australia is developing and implementing a broad process for ecological assessment in a risk framework. This process is referred to as ecological risk assessment and explicitly identifies five ecological components for analysis: target species, non-target species comprising by-product (predominantly retained) and by-catch (predominantly discarded), threatened species, fish habitats, and ecological communities. Within each component, for each type of fishing method separately, the approach involves a three-levelled hierarchical process of assessment, with increasing data requirements and complexity when progressing from level 1, through level 2, to level 3 assessment. Level 1 assessment involves expert judgement and determines whether or not there is a need to progress to level 2 or, alternatively, to implement a management response. Level 2 assessment is semi-quantitative and determines whether or not there is a need to progress to level 3 or, alternatively, to implement a management response. When progressing from one level to the next, depending on costs, there is the choice of either immediately initiating a management response to ameliorate risk of adverse effects or, alternatively, proceeding to invest in research and monitoring to enable a higher level of assessment (Hobday et al. 2006; Smith et al. 2006). This approach to ecological risk assessment would be exhaustive if all components were taken to level 3 and would require excessive costs in a multispecies fishery.

The purpose of the present study is simply to take a single chondrichthyan species — the piked spurdog (*Squalus megalops*) — for which sufficient data are available to undertake an assessment at each of the three levels and to evaluate the suitability of the approach for chondrichthyan species in general. *Squalus megalops* falls within the non-target component and is one of the most abundant and widespread chondrichthyan species impacted by Australia's Southern and Eastern Scalefish and Shark Fishery (SESSF). The species is mostly taken as by-catch by demersal trawl on the continental shelf and upper slope (~600 tonnes (t) per annum) (Walker and Gason 2006). Small quantities are also taken on the upper slope by automatic longline targeted at teleost species and on the continental shelf by gillnets deployed in the targeted shark fishery for *M. antarcticus* (Walker and Gason 2005; Walker et al. 2005). Because of long-term declines in abundance of shark and chimaera populations off New South Wales, southeastern coast of Australia (Graham et al. 2001), quota reductions on target and by-product shark and chimaera species, and growing consumer demand for shark meat, some large individuals of *S. megalops* are beginning to be retained for marketing (Walker and Gason 2005).

Materials and methods

Squalus megalops was assessed using the Australian process for ecological risk assessment as part of the non-target component at each of the three hierarchical levels. Progressing through the three levels, level 1 involved qualitative assessment based on expert judgement, level 2 involved semi-quantitative assessment, and level 3 involved fully quantitative assessment based on available data. The approaches to level 1 and level 2 assessments are explicitly prescribed (Hobday et al. 2006), and Australia has extensive experience with stock assessment of target and by-product species in a risk framework (level 3 assessment). However, the process is not presently explicit for level 3 assessment of non-target species where catches are not known precisely. The present study applies an approach that assumes no knowledge of catches and catch rates.

Table 1. Description of the potential impacts of different fishing activities on *S. megalops*.

Impact	Fishing activity
Direct	Capture (damage or mortality due to gear deployment, including discards)
	Cryptic mortality (unaccounted damage or mortality due to interactions with fishing gear)
	Gear loss (damage or mortality without capture due to interactions with gear lost from the fishing vessel)
Indirect	Species translocation (introduction of species to the habitat of the assessed species)
	On-board processing and catch discarding (discard of unwanted parts of target species or unwanted organisms from the catch)
	Provisioning (use of bait or burley)
	Pollution (introduction of chemical and physical pollutants from fishing vessels, such as exhaust, oil spills, detergents, rubbish, lost gear, noise)

Note: Direct impacts are impacts causing damage or mortality, whereas indirect impacts are impacts altering the habitat of the species (adapted from Hobday et al. 2006).

Level 1 assessment

Level 1 assessment was a qualitative analysis for each fishing method that may impact *S. megalops* based on expert knowledge (J.M.B. and T.I.W.). Adopting the precautionary approach, the species was assigned the highest risk value if there was uncertainty about risk judgement (Hobday et al. 2006). The fishing methods in the SESSF that may have an effect on *S. megalops* in southern Australia are otter trawl and Danish seine nets, demersal shark gillnets, demersal shark longlines, automatic longlines, droplines, and traps and pots. Within these fishing methods, seven associated activities (explained in Table 1) may impact *S. megalops*. Each fishing-related activity within the non-target component was assessed using spatial- and temporal-scale, intensity, and consequence analyses (Hobday et al. 2006). This approach involved assigning a score to each of spatial and temporal scale, intensity, and consequence of the fishing activity (explained in Table 2). Fishing methods with fishing activities with a consequence score ≤2 were eliminated from further assessments, whereas methods with higher scores underwent more in-depth assessment at level 2.

Level 2 assessment

For level 2, the species was assessed based on its biological

Table 2. Description of the score values for the spatial and temporal scale and intensity and consequence of the fishing activities (adapted from Hobday et al. 2006).

Score	Spatial scale (nm)	Temporal scale	Intensity	Consequence
1	<1	Decadal	Negligible (remote likelihood of detection)	Negligible (impact unlikely to be measured)
2	1–10	Every several years	Minor (seldom occurring and rare to detect)	Minor (minimal impact on stock size, structure, or dynamics)
3	10–100	Annual	Moderate (moderate at broader scale, or severe but local)	Moderate (medium impact on stock size, structure, or dynamics)
4	100–500	Quarterly	Severe (severe and occurring often at broad scale)	Major (wider and longer term impact on stock size, structure, or dynamics)
5	500–1000	Weekly	Major (occasional but very severe and localized or frequent and widespread but less severe)	Extreme (serious impact on stock size, structure, or dynamics with long time period to restore to acceptable levels)
6	>1000	Daily	Catastrophic (local to regional severity or continual and widespread)	Intolerable (widespread and irreversible impact on stock size, structure, or dynamics)

productivity and catch susceptibility. Biological productivity can be inferred from the reproductive rate or the natural mortality rate of a species assuming that with immigration and emigration being equal, there has to be a balance between reproductive rate and natural mortality rate for a population to remain in equilibrium (Walker 2004). Species with low reproductive rate and low natural mortality have low biological productivity and, hence, are at higher risk from the effects of fishing than species with high biological productivity. For *S. megalops*, natural mortality (M) was used as a proxy for biological productivity. Natural mortality was estimated by five indirect life-history methods described elsewhere (e.g., Cortés 2002), and the mean value was used. The indirect methods of Pauly (1980), Hoenig (1983), and Chen and Watanabe (1989) and two methods by Jensen (1996) use parameters estimated from the von Bertalanffy growth model (VBGM) and maximum age information obtained from Braccini (2006) for *S. megalops*. Pauly's (1980) method also uses information on the mean value of water temperature (14.6 °C) that was taken from http://www.marine.csiro.au. Based on empirical data, Walker (2004) devised a scale for M categorization where values of $M \leq 0.16$, between 0.16 and 0.38, and ≥ 0.39 correspond to low, moderate, and high biological productivity, respectively. This scale was used for biological productivity categorization of *S. megalops*.

Catch susceptibility, a measure of the extent of the fishing impact of each fishing method, is the product of availability (proportion of the spatial distribution of the population that is fished by the fishing method, based on the assumption of an even distribution of fishing method and species), encounterability (proportion of the available population encountered by one unit of fishing effort), selectivity (proportion of the encountered population that is captured by the fishing gear), and post-capture mortality (proportion of captured animals that die) (Walker 2004). Each of these fishing parameters ranges from 0 to 1; hence, catch susceptibility also ranges from 0 to 1. Fishing parameters with assigned values of 0.33, 0.66, and 1.00 (upper value for each one-third range) are designated low, moderate, and high, respectively (Table 3; Walker 2004). Based on expert judgement and the precautionary approach (i.e., high if unknown), the availability, encounterability, selectivity, post-capture mortality, and catch susceptibility of *S. megalops* were determined for each fishing method.

A species identified as having low biological productivity with moderate to high catch susceptibility would be considered to be at high risk and need to be assessed at level 3. A species with moderate to high biological productivity and low catch susceptibility would be considered to be at low risk and require no further assessment.

Level 3 assessment

Level 3 assessment involved a quantitative data-intensive analysis. Application of biomass dynamic models or more complex models requires time series of catch, fishing effort, and relative abundance data, which are not available for most shark species, particularly by-catch species. Given that demographic analyses require only life-history parameters, which are commonly available for many species, this approach was used to make the assessment more compatible and applicable to a broader suite of fisheries. The assessment involved the quantitative estimation of population growth rate, elasticities, rebound potential, and population doubling time.

Population growth rate ($\lambda = e^r$, where r is the population instantaneous rate of increase) and elasticities (effect of a proportional change in a vital rate on population growth rate) were estimated using a birth-flow Leslie matrix (Caswell 2001). Elasticities of fertility, juvenile survival, and adult survival are normally obtained by summation of matrix element elasticities across relevant age classes (e.g., Caswell 2001; Carlson et al. 2003). However, in the present study, age-at-maturity of *S. megalops* was not assumed to be knife-edged, rather it was determined from an ogive produced by

Table 3. Description of the score values of fishing parameters for three arbitrary risk categories (adapted from Walker 2004).

Parameter	Risk category		
	Low	Moderate	High
Availability	0.33 (fishery ranges < one-third of species range)	0.66 (fishery ranges one-third to two-thirds of species range)	1.00 (fishery ranges > two-thirds of species range)
Encounterability	0.33 (0–0.33 probability of species encountering the gear, e.g., pelagic species encountering bottom trawl net)	0.66 (0.33–0.66 probability of species encountering the gear, e.g., pelagic species encountering mid-water trawl net)	1.00 (0.67–1.00 probability of species encountering the gear, e.g., bottom-dwelling species encountering bottom trawl net)
Selectivity	0.33 (0–0.33 probability of species being caught by the gear, e.g., filter-feeder species taking a baited hook)	0.66 (0.33–0.66 probability of species being caught by the gear, e.g., fast-swimming species taken by bottom trawl net)	1.00 (0.67–1.00 probability of species being caught by the gear, e.g., species with protruding structures taken by gillnet)
Post-capture mortality	0.33 (0.67–1.00 probability of survival after capture, e.g., discarded bottom-dwelling species with spiracles and robust structure)	0.66 (0.33–0.66 probability of survival after capture, e.g., discarded species with a fragile structure and ram-jet ventilation)	1.00 (0–0.33 probability of survival after capture, e.g., retained target and by-product species)
Catch susceptibility	0–0.33	0.33–0.66	0.67–1.00

Note: Catch susceptibility is the product of availability, encounterability, selectivity, and post-capture mortality.

Braccini et al. (2006). Hence, for each age class, the survival elasticity of juveniles and adults was the product of the elasticity and the proportion of juvenile and adult females within each class. The total juvenile and adult elasticity was then obtained by summing across the different age classes. Population rebound potential (r_z, where z is total mortality) and doubling time ($T_D = \ln(2)\cdot r_z^{-1}$) were estimated by the method of Smith et al. (1998), which incorporates density-dependent compensation of adult M through preadult survival. Rebound potential is calculated at the population level of maximum sustainable yield (Smith et al. 1998).

To explore sensitivity to error and (or) variation in life-history parameter estimates, a probability density function (pdf) was developed for each life-history parameter following the approach of Cortés (2002) and Carlson et al. (2003). The pdfs were then used in a Monte Carlo simulation (with 10 000 iterations) to incorporate uncertainty in the estimation of population parameters. Each iteration involved the random selection of a set of life-history parameter values and the calculation of λ, elasticities, r_z, and T_D. In this way, prediction intervals (2.5th and 97.5th percentiles) were obtained from the probability density distribution for each of the estimated population parameters. Simulations were run using Microsoft Excel spreadsheets equipped with the add-in PopTools version 2.6 (http://www.cse.csiro.au/poptools/) and a risk assessment software (Crystal Ball; Decisioneering Inc., Denver, Colorado) lent by E. Cortés (NOAA, Southeast Fisheries Science Centre, Panama City, Florida).

Life-history parameters needed for the estimation of population parameters were obtained from the literature. Average litter size, the relationship between fecundity and total length (TL) of female, embryo sex ratio, length-at-maturity, and length-at-maternity (relationship between the proportion of females in maternal condition, i.e., contributing to annual recruitment, and TL) were obtained from Braccini et al. (2006). Average litter size was assumed to follow a normal pdf with a mean (and standard deviation, SD) of 2.32 (0.48) and a lower and upper bounds of 2 and 4, respectively, reflecting the range of litter sizes reported. The fecundity–TL relationship was predicted from the linear equation, litter size = 0.0071(0.001)TL – 1.503(0.549), and the error structure around estimates of fecundity parameters was represented by a normal pdf. The embryo sex ratio reported for *S. megalops* was 1:1 so a 0.5 factor was used to half the litter size–TL function and obtain the number of female embryos per female. Length-at-maternity was predicted from the following logistic equation:

$$\text{proportion maternal} = 0.5(1 + e^{-\ln(19)(\mathrm{TL}-531(18))/(626(47)-531(18))})^{-1}$$

and the error structure around estimates of maternity parameters was represented by a normal pdf. Growth parameters and maximum age were obtained from Braccini (2006). The growth equation for females was used to transform the relationships between the reproductive variables and TL to relationships between reproductive variables and age. Natality-at-age was calculated as the product of 0.5 (embryo sex ratio), the age-at-fecundity, and the age-at-maternity functions. Two extreme case scenarios were considered. The first is deemed as the worst-case scenario, whereas the second scenario is the more optimistic.

In the first scenario, growth parameters (and standard error, SE) L_∞ = 756 (45) mm, k = 0.042 (0.005) year^{-1}, and t_0 = –9.77 (1.30) years produced by a two-phase VBGM were used as the most likely values in a normal pdf. The error structure around estimates of age at 50% maturity was represented by a triangular pdf with 15 as the most likely value and ±2 years as the lower and upper bounds. These values were derived from a length-at-maturity curve (Braccini et al. 2006) and the growth curve produced by the two-phase VBGM. The error structure around estimates of maximum age was represented by a linearly decreasing pdf scaled to 1, with the most likely value of 28 (oldest shark aged by Braccini 2006) and the lower bound set by arbitrarily adding 30% to the most likely value, i.e., 36 (Cortés 2002). Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.862 to 0.936, estimated by the Hoenig (1983) and Jensen (1996) methods, respectively. Adult M for the Smith et al. (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.149. Maximum sustainable yield for the Smith et al. (1998) method was assumed to occur at total mortality (Z) = 1. 5M.

In the second scenario, growth parameters L_∞ = 699 (17) mm and k = 0.056 (0.005) year^{-1} produced by a two-parameter VBGM growth model were used as the most likely values in a normal pdf. The error structure around estimates of age at 50% maturity was represented by a triangular pdf with 14 as the most likely value and ±2 years as the lower and upper bounds. These values were derived from the length-at-maturity curve and the growth curve produced by the two-parameter VBGM growth. Maximum age was represented as in the first scenario, with the difference that the maximum bound was set to 50% of the most likely value, i.e., 42. Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.930 to 0.936, estimated by the Chen and Watanabe (1989) and Jensen (1996) methods, respectively. Adult M for the Smith et al. (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.072. Maximum sustainable yield for the Smith et al. (1998) method was assumed to occur at $Z = 2M$.

A Spearman rank correlation (r_S) was used to measure possible correlation between life-history parameters and λ. For each scenario, the correlation between the simulated M, k, the slope of the fecundity curve, and TL at 50% maturity of the length-at-maternity relationship with the forecasted λ was determined. A modified Bonferroni method was used to correct for multiple hypothesis testing (Jaccard and Wan 1996). Individual comparisons were rank-ordered from most to least significant and a significance cutoff for the most significant correlation was determined by dividing the significance level of 0.05 by 8, the number of comparisons made. If the most significant correlation was found to be significant, a new significance cutoff for the second most significant correlation was determined by dividing the significance level of 0.05 by 7. This stepwise backwards elimination procedure was used for determining the significance cutoff for the remainder of the correlations.

Results

Level 1 assessment

Level 1 assessment of the fishing methods indicated that the only fishing-related activity to have moderate or higher consequences on the sustainability of *S. megalops* was that associated with "capture fishing" (Appendix A, Table A1). Other activities had either negligible or minor consequences. Among methods, capture fishing of shark longlines, droplines, and traps and pots had a negligible effect on *S. megalops* because of their recent decline to ~0 effort in 2004 (Walker and Gason 2006). Hence, these methods were not assessed at a second level. Conversely, capture fishing for the otter trawl, Danish seine, shark gillnet, and automatic longline methods had a consequence score >2, so these fishing methods need to be assessed at level 2.

Level 2 assessment

Estimates of natural mortality (M) had a mean value of 0.085, ranging from 0.066, for one of Jensen (1996) methods, to 0.149 (Hoenig 1983), indicating that *S. megalops* had low biological productivity (i.e., $M \le 0.16$). Catch susceptibility of *S. megalops* varied depending on the fishing method (Appendix A, Table A2). For the shark gillnet method, given the low selectivity and moderate availability and post-capture mortality, catch susceptibility was low (catch susceptibility = 0.66 × 1.00 × 0.33 × 0.66 = 0.14). For the automatic longline method, catch susceptibility was also low, as availability was low (catch susceptibility = 0.33 × 1.00 × 1.00 × 0.66 = 0.22). For the otter trawl and Danish seine methods, there is uncertainty regarding the extent of their spatial overlap with *S. megalops* distribution. If availability for these fishing methods was designated low, catch susceptibility was also low (catch susceptibility = 0.33 × 1.00 × 1.00 × 1.00 = 0.33). However, if availability was considered moderate, catch susceptibility was also moderate because of high encounterability, selectivity, and post-capture mortality (catch susceptibility = 0.66 × 1.00 × 1.00 × 1.00 = 0.66). In addition, cumulative effects across the four fishing methods may cause an underestimation of total catch susceptibility; hence, based on *S. megalops* low biological productivity, this species was classed as at high risk and needed to be assessed at level 3.

Level 3 assessment

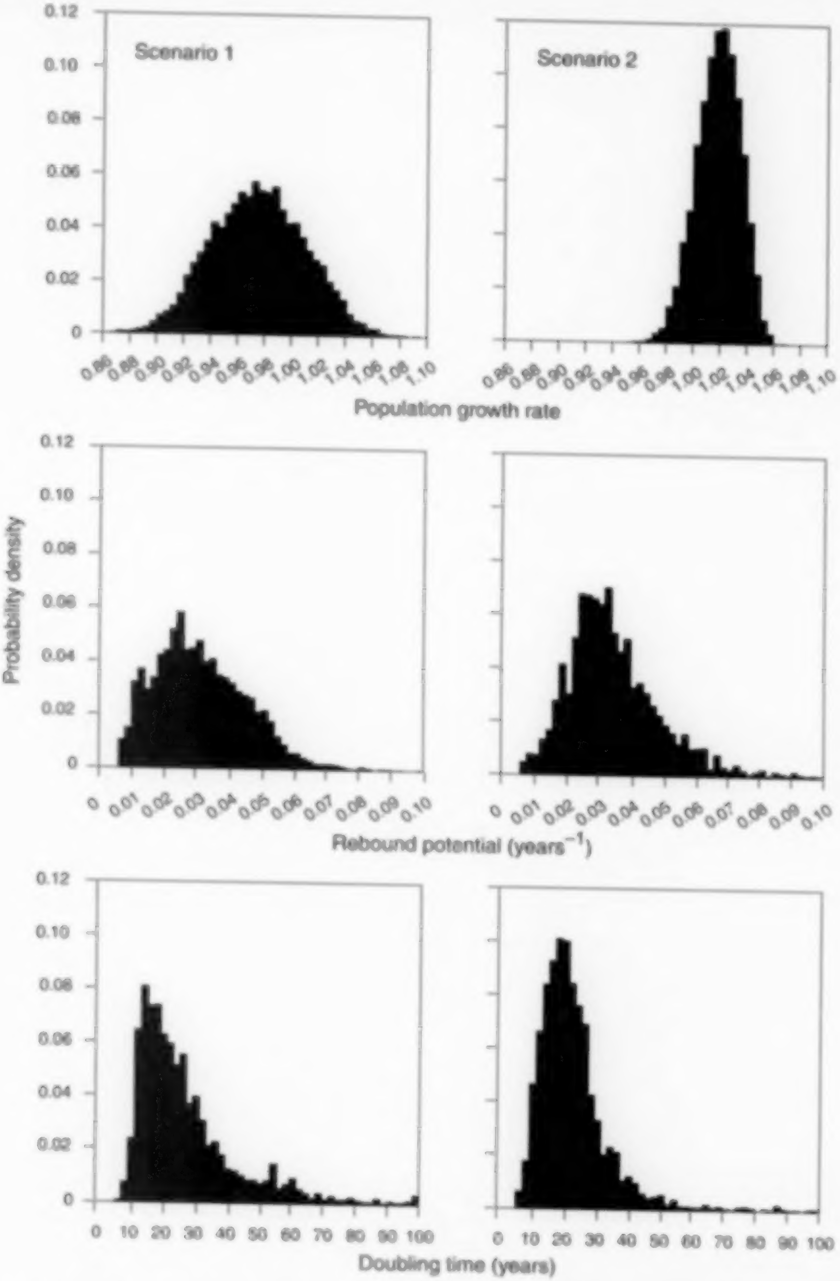
For the first (worst-case) scenario, population growth rate (λ) averaged 0.975 (median 0.974, 95% confidence interval (CI) 0.974–0.976) (Fig. 1). Fertility elasticities averaged 0.046 (0.045, 0.046–0.046), elasticities of juvenile survival were 0.630 (0.629, 0.628–0.631) and those of adults were 0.325 (0.325, 0.323–0.326). Rebound potential (r_Z) averaged 0.031 year^{-1} (0.029, 0.030–0.032) and population doubling time (T_D) was 28.2 years (23.5, 27.9–28.5) (Fig. 1). There was a negative correlation between M and λ ($r_S = -0.685$, $P = 0.006$) and between TL_{50} (TL at 50% maturity) and λ ($r_S = -0.139$, $P = 0.025$). There was a positive correlation between the growth coefficient (k) and λ ($r_S = 0.474$, $P = 0.008$) and between the fecundity slope and λ ($r_S = 0.284$, $P = 0.017$).

For the second (more optimistic) scenario, λ averaged 1.018 (median 1.019, 95% CI 1.017–1.019) (Fig. 1). Fertility elasticities averaged 0.045 (0.045, 0.045–0.045), elasticities of juvenile survival were 0.397 (0.395, 0.396–0.398) and those of adults were 0.559 (0.560, 0.558–0.560). Rebound potential averaged 0.035 year^{-1} (0.032, 0.035–0.035) and T_D was 23.7 years (21.4, 23.5–23.9) (Fig. 1). There was a negative correlation between M and λ ($r_S = -0.111$, $P = 0.050$) and between TL_{50} and λ ($r_S = -0.314$, $P = 0.013$). There was a positive correlation between k and λ ($r_S = 0.342$, $P = 0.010$) and between the fecundity slope and λ ($r_S = 0.638$, $P = 0.007$).

Discussion

Conservation and management of marine resources should be based on the integration of qualitative and quantitative methods (Cortés 2004) simply because management based solely on quantitative information is of limited application to data-poor fisheries (Johannes 1998). Qualitative, semi-quantitative, and quantitative data together in a hierarchical assessment framework showed that *S. megalops* is potentially

Fig. 1. Probability density distribution of population growth rate, rebound potential, and population doubling time for scenarios 1 and 2 (N = 10 000 simulations).



highly susceptible to the effects of fishing. At a qualitative level (level 1), the hierarchical assessment allowed screening out of fishing methods and fishing-related activities considered to pose low risk to this species. This indicates that research effort should be allocated to those fishing methods and fishing activities (capture fishing) leading to moderate or higher impacts on *S. megalops*. At this level, expert opinion should include a range of stakeholders who understand the interactions between fishing methods and the biology of the species (scientists, managers, fishers). Qualitative expert judgement, e.g., knowledge possessed by artisanal fishers, has been valuable for successful management of tropical fisheries in developing countries (Johannes 1998). Furthermore, expert knowledge is commonly used in Bayesian (e.g., Martin et al. 2005) and fuzzy logic (Cheung et al. 2005) modelling for conservation assessments. Hence, quantitative information need not be an exclusive condition for sound management; a qualitative assessment of chondrichthyans would allow ruling out of species ranked at low risk, allowing focus on those at high risk. The value of this approach is twofold. First, it is usually not practical to undertake long-term studies on non-target chondrichthyan species because of an urgent need for their effective management. Second, the Australian ecological risk assessment process is valuable at making research more cost-effective and at prioritising research funding involving high costs associated with collecting quantitative fishing data (Dulvy et al. 2003). An important feature of the process is that it provides the option for a management response at any level. This is essential because most fisheries impact far more species than can ever be investigated by full stock assessment. In southern Australia, for example, full stock assessments have been undertaken on only a dozen or so species taken by trawl, gillnets, and longlines, yet hundreds of species of marine chondrichthyans, teleosts, invertebrates, mammals, birds, and reptiles are impacted. This approach will be particularly useful for developing countries where two-thirds of reported landings of chondrichthyans occurred (Bonfil 1994), resources for monitoring fishery impacts are limited (Johannes 1998), and plans of management have not been implemented.

A semi-quantitative assessment (level 2) ranked *S. megalops* at high risk given its low biological productivity and the cumulative catch susceptibility to the fishing methods. Musick (1999) proposed a productivity scale for ranking extinction risk of marine fish based on the intrinsic rate of increase, the growth coefficient (k), fecundity, age-at-maturity, and maximum age. Using either Musick's (1999) or the natural mortality (M) (present study) criteria, *S. megalops* is ranked as a low productive species. Hence, for rapid assessment at level 2, M is considered a good proxy to productivity.

Squalus megalops had moderate catch susceptibility due to cumulative effects of the different fishing methods used in southeastern Australia. Shark gillnets and Danish seines are used on the continental shelf, whereas otter trawlers operate on the upper slope throughout the SESSF and on the shelf off New South Wales, far eastern Victoria, and eastern Tasmania. When considered separately, each of the three fishing methods has low availability, but the three methods together have medium availability and therefore may increase the catch susceptibility of *S. megalops*. In addition, the availability to the otter trawl method would be high if the population is predominantly distributed on the upper continental slope. Demersal trawling may create a higher food supply by disturbing sediments and exposing prey, attracting *S. megalops* to the fishing grounds as this species of shark is an opportunistic predator that consumes a wide range of prey items (Braccini et al. 2005). When applied to a large number of species, the advantage of this approach is to allow low-risk species to be excluded from the data-intensive quantitative analysis of level 3, such that research and management efforts can be directed where most needed (Stobutzki et al. 2002; Hobday et al. 2006). Even for data-poor fisheries, where species-specific information on biological productivity or catch susceptibility is not available, this level of analysis can be applied. Information can be used from studies from other areas or on closely related species (Walker 2004) with the caution that there may be some degree of geographical variation in life-history parameters (e.g., Parsons 1993) and catch susceptibility parameters.

There are some caveats to the application of level 1 and level 2 assessments. Rejection of the methodology, particularly at level 1, will require underestimating the risk of depletion likely to occur for species with high uncertainty in score values for the different fishing impacts. However, this is minimized as the method adopts a precautionary approach, penalizing uncertainty and ranking those species for which little information is available as at risk. Risk overestimation may occur for these species at level 1, creating the need for data collection and assessment of productivity and catch susceptibility. Strong favourable opinions at levels 1 and 2 may also lead to underestimation of risk by limiting further species assessment. Therefore, objective assessment of species at these levels is critical to the performance of the methodology.

A quantitative assessment (level 3) showed that population growth of *S. megalops* is slow even under the assumption of density-dependent compensation after a fishing exploitation rate equal to the natural mortality rate. For both the best- and worst-case scenarios, the estimations of rebound potential (r_z) and population doubling time (T_D) are low even within the range reported for shark species (0.017–0.136 $year^{-1}$ and 5.1–41.5 years, respectively) and are similar to the values reported for the spiny dogfish (*S. acanthias*) from the northwestern Atlantic (Smith et al. 1998). Population growth rate (λ) was also slow, placing *S. megalops* towards the "slow" end of the spectrum along a continuum of life-history traits of sharks (Cortés 2002). For the worst-case scenario, most simulated λ values fell below 1, suggesting population decrease even under no fishing mortality. *Squalus acanthias* and the shortspine spurdog (*S. mitsukurii*) also show λ values below 1 and would not possess the biological attributes to restore λ to its original level after moderate exploitation (Cortés 2002). For the worst-case scenario proposed for *S. megalops*, λ values below 1 would result from the negative correlation between λ and M and the positive correlation between λ and k. Within this scenario, some of the permutations of the combined M and k that can be obtained from their respective distributions (in this case high M and low k values) resulted in λ values below 1 (McAllister et al. 2001). Elasticities of juvenile and adult survival were higher than fertility elasticities, indicating that λ is more sensitive to the survival of juveniles and adults. As for *S. acanthias* and *S. mitsukurii* (Cortés 2002), for the worst-case scenario, juvenile *S. megalops* had a higher elasticity than adults, and management actions should focus on the protection of juveniles. For the best-case scenario, because of the simulated longer life span (42 years) and the larger number of adult age classes, elasticity of adults was higher for what management actions should focus on this latter group. In all, the estimated values of r_z, T_D, and λ indicate that recovery time of *S. megalops* population after fishing overexploitation is expected to be very long. Although the relative abundance of *S. megalops* has remained stable off New South Wales (Graham et al. 2001), probably because of refuge areas where ground is untrawlable (Graham 2005), this is currently the most caught by-catch shark species taken by demersal trawlers in southeastern Australia. Trends in catch per unit effort from onboard scientific observer data suggest that the population has been stable during 1992–2005 (Walker and Gason 2006). Nevertheless, the aggregating behaviour of *S. megalops* (Graham 2005), in combination with its slow growth rate (Braccini 2006) and low reproductive output (Braccini et al. 2006), makes this species potentially vulnerable to the effects of fishing. For species with similar life-history traits, such as *S. acanthias*, stock depletions have been well documented (e.g., Holden 1977). Hence, any increase in catch susceptibility through targeting, increased retention of catch, or change in gear design such as reducing mesh size of shark gillnets could quickly increase the risk of stock depletion for *S. megalops*. Conservation and management for sustainable use of *S. megalops* will require a close control of fishing mortality because of the low biological productivity of this species.

In summary, the hierarchical ecological risk assessment approach adopted in Australia allows for the effective evaluation of the effects of fishing on non-target chondrichthyan species and the identification of species at risk. Under this approach, research and management effort can be prioritised and directed to where it is most needed. The hierarchical approach allows for management response at any level as an alternative to undertaking the research required to proceed to the next level of assessment. Hence, this approach is particularly useful for fishery management organizations for the assessment of data-limited fisheries. For example, the Australian Fisheries Management Authority (AFMA) is presently applying the approach for the evaluation of 14 fisheries as the basis for determining priorities for research, fishery monitoring, and management (Hobday et al. 2006). There is no doubt about the need for management of chondrichthyans, particularly for those taken as by-catch in multispecies fisheries: the question is how to make research and management more cost-effective and priority-driven when chondrichthyan resources are being depleted and there is insufficient time or funding available for comprehensive data collection on all species.

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Appendix A

Tables A1 and A2 follow.

Table A1. Level 1 assessment of the fishing methods having a potential impact on *S. megalops*.

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
(*a*) Otter trawl and Danish seine methods							
Capture	1	6	6	4	3	1	*S. megalops* is captured by trawl nets throughout the range of the fishery. Moderate impact on stock as there has been no long-term decline in relative abundance in one region of the fishery (Graham et al. 2001); however, for the other regions, there is no long-term relative abundance information.
Cryptic mortality	1	6	6	2	2	2	Cryptic mortality caused by escapement of animals injured from encounters with trawl nets may happen but it is considered to have a minor impact on the stock. Certainty low because of difficulties in measuring this impact.
Gear loss	1	6	6	1	1	1	Trawl net loss is a rare event because of their high price, creating a high incentive not to loose them and to retrieve them.

Table A1 (*continued*).

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Species translocation	1	6	6	1	1	1	Invertebrate and vertebrate species caught in trawl nets can be translocated up to several miles between shots but it is unlikely to have a measurable impact on the stock through habitat modification.
On-board processing and catch discarding	1	6	6	3	3	2	Moderate to large quantities of organisms are discarded in trawling operations. This practice can attract opportunistic species, such as *S. megalops* (Braccini et al. 2005), increasing the probability of being taken by the gear. However, the extent of this impact is uncertain because of a lack of data.
Provisioning	0					1	Provisioning does not occur in this method.
Pollution	1	6	6	2	1	1	Chemical or physical pollutants might have minor risks as this hazard only affects a small area and *S. megalops* is a mobile species with an avoidance ability > scale of the hazard. Impact on stock is considered negligible.
(*b*) Shark gillnet method							
Capture	1	6	6	3	4	1	Shark gillnets (6–6.5 inch mesh size) are designed to target larger-sized species (e.g., *M. antarcticus*), so only large female *S. megalops* are taken throughout the range of the fishery (Walker et al. 2005). Selective removal of significant numbers of large females could have a major impact on the stock.
Cryptic mortality	1	6	6	2	2	2	Refer to part *a*.
Gear loss	1	6	6	1	1	1	Refer to part *a*.
Species translocation	1	6	6	1	1	1	Refer to part *a*.
On-board processing and catch discarding	1	6	6	3	3	2	Refer to part *a*.
Provisioning	0					1	Refer to part *a*.
Pollution	1	6	6	2	1	1	Refer to part *a*.
(*c*) Automatic longline method							
Capture	1	6	6	3	3	2	This fishing method is used across a broad spatial and temporal scale but only in deepwater (continental slope) where *S. megalops* is not very abundant; hence, the impact on the stock is considered moderate.
Cryptic mortality	1	6	6	2	2	2	Refer to part *a*.
Gear loss	1	6	6	1	1	1	Refer to part *a*.
Species translocation	1	6	6	1	1	1	Refer to part *a*.

Table A1 (*concluded*).

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
On-board processing and catch discarding	1	6	6	2	2	1	Discards in this fishery are minimal, having a minor effect on the stock.
Provisioning	1	6	6	2	2	1	The most commonly used bait is squid, which is harvested at low levels with minor consequence for the stock of squid and, hence, minor indirect effect on *S. megalops* stock.
Pollution	1	6	6	2	1	1	Refer to part *a*.

Note: Presence score: 1, present; 2, absent. Certainty score: 1, certain (data exist and considered sound); 2, uncertain (no data or considered poor or conflicting; see Table 2 for score value description).

Table A2. Catch susceptibility for otter trawl and Danish seine method, shark gillnet method, and automatic longline method.

	Parameter					
Fishing method	Av	Ec	Se	Pc	Cs	Rationale
Otter trawl and Danish seine	L–Mo	H	H	H	L–Mo	This method is confined to the continental shelf and upper slope overlapping in part with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species. Selectivity is high given uncertainty in selectivity of trawl nets. Post-capture mortality is also high because of trauma caused inside the net.
Shark gillnet	Mo	H	L	Mo	L	This method is confined to the continental shelf, mostly inside the 120–150 m isobath, with moderate overlap with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species. Selectivity is low because of the 6–6.5 inch mesh size of the gillnet (see Walker et al. 2005, table 6).
Automatic longline	L	H	H	Mo	L	This method is confined to the continental slope with very low overlap with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species as *S. megalops* is likely to take the baited hook, given its opportunistic feeding behaviour. Selectivity is high given that hook size does not affect catch (see Walker et al. 2005).

Note: Risk categories of availability (Av), encounterability (Ec), selectivity (Se), post-capture mortality (Pc), and catch susceptibility (Cs) are L (low, 0.33), Mo (moderate, 0.66), and H (high, 1.00).

Long-term response of daily epilimnetic temperature extrema to climate forcing

Susann Wilhelm, Thomas Hintze, David M. Livingstone, and Rita Adrian

Abstract: Twenty years (1983–2002) of hourly summer temperature data from the epilimnion of Müggelsee, a shallow lake in northern Germany, showed a long-term increase, with the rate of increase of the daily minima (nighttime temperatures) exceeding that of the daily maxima (daytime temperatures). This does not simply reflect the long-term behaviour of air temperature, which did not exhibit a significant degree of day–night asymmetry. A sensitivity analysis based on a heat-balance model revealed that the daily extrema of the lake surface equilibrium temperature responded differently not only to shifts in air temperature, but also to shifts in wind speed, relative humidity, and cloud cover, suggesting that long-term changes in all four variables contribute to day–night asymmetry in the epilimnetic temperature. A comparison of nighttime and daytime estimates of the heat flux components into the lake indicates that the emission of long-wave radiation from the atmosphere is likely to be the main process responsible for day–night asymmetry in the epilimnetic temperature. Although this process is partially dependent on air temperature, it is also dependent on relative humidity and cloud cover. The influence of long-term changes in these additional driving variables on epilimnetic temperatures cannot therefore be neglected.

Résumé : Des séries horaires de données de température d'été sur 20 ans (1983–2002) dans l'épilimnion de Müggelsee, un lac peu profond du nord de l'Allemagne, montrent une augmentation à long terme de la température, dont le taux d'accroissement des minimums journaliers (températures nocturnes) surpasse celui des maximums journaliers (températures diurnes). Cela ne reflète pas simplement le comportement à long terme de la température de l'air, qui ne montre pas un degré significatif d'asymétrie jour–nuit. Une analyse de sensibilité basée sur un modèle de bilan thermique indique que les extrêmes journaliers de l'équilibre thermique à la surface du lac réagissent différemment non seulement aux changements de température de l'air, mais aussi aux changements de vitesse du vent, d'humidité relative et de couverture nuageuse; cela laisse croire que des changements à long terme de ces quatre variables contribuent à l'asymétrie jour–nuit de la température de l'épilimnion. Une comparaison des estimations des composantes du flux thermique dans le lac durant le jour et durant la nuit indique que l'émission de radiation à grande longueur d'onde dans l'atmosphère est vraisemblablement le processus principal responsable de l'asymétrie de la température de l'épilimnion. Bien que ce processus soit partiellement dépendant de la température de l'air, il est aussi dépendant de l'humidité relative et de la couverture nuageuse. L'influence des changements à long terme de ces variables explicatives additionnelles ne peut donc pas être négligée.

[Traduit par la Rédaction]

Introduction

Over large areas of the earth's surface, long-term warming is known to be proceeding faster at night than during the day (e.g., Karl et al. 1993; Kukla and Karl 1993), probably as a result of an increase in low-level cloud cover associated with an increase in air pollution (Dai et al. 1999; Satheesh et al. 1999). There is some evidence that terrestrial biota may already be responding to such asymmetric air temperature increases involving anomalously high rates of nocturnal warming. The primary production of the dominant native C_4 grass *Bouteloua gracilis* in Colorado, for instance, is decreasing as a result of nocturnal warming, whereas the abundance and production of exotic and native C_3 forbs is increasing (Alward et al. 1999). Nocturnal warming has also been shown to result in an increase in the dark respiration of the tree *Populus deltoides* (Turnbull et al. 2004) and a rise in the rate of development of the cabbageworm *Pieris rapae* (Whitney-Johnson et al. 2005).

Empirical studies show that water temperatures close to the surface of lakes closely follow ambient air temperatures (e.g., McCombie 1959; Shuter et al. 1983; Livingstone and

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Lotter 1998). The results of model studies predicting that rising air temperatures will result in increasing epilimnetic temperatures (e.g., Hondzo and Stefan 1993; Stefan et al. 1998; Peeters et al. 2002) are supported by the existence of long-term historical data series demonstrating that, over the past few decades, such increases have indeed occurred (e.g., Schindler et al. 1990; Gerten and Adrian 2002*a*; Livingstone 2003). However, despite the likelihood that the rise in epilimnetic temperature may be more closely related to nighttime processes, such as the inhibition of nighttime cooling, than to daytime processes (Livingstone 2003), very little work has been done on analysing the impact that day–night asymmetry in rising air temperatures might have on the long-term warming of lake epilimnia. Specifically, there is a lack of knowledge on whether day–night asymmetry involving a long-term decrease in the daily temperature range might also be present in lake epilimnia, although lake biota would be likely to respond to such a phenomenon. The present study attempts to rectify this omission.

One of the areas with a marked degree of day–night asymmetry in long-term regional warming is central Europe (e.g., Heino et al. 1999). Here, we examine a unique 20-year set of hourly air and water temperature data recorded between 1983 and 2002 for Müggelsee, a shallow, polymictic lake in northern Germany, with a view to investigating the long-term behaviour of the daily water temperature extrema and their relationship to that of the daily air temperature extrema. We focus on the months of June, July, and August, when the diel cycle in epilimnetic temperature is most pronounced and when the daily maximum approaches the tolerance threshold for some aquatic species. To ascertain the meteorological driving factors most likely to be responsible for long-term changes in the daily epilimnetic temperature extrema, and hence in the daily epilimnetic temperature range, a sensitivity analysis based on the heat budget and equilibrium temperature approach of Edinger et al. (1968) is performed.

Materials and methods

Study site

Müggelsee is a shallow, eutrophic lake situated 34 m above sea level (a.s.l.) in Berlin, Germany (52°26′N, 13°39′E). It has a mean depth of 4.9 m, a maximum depth of 8 m, and covers an area of about 7.3 km^2. It is one of the intercalated lakes of the River Spree, with an average residence time of 6–8 weeks. Within the last 25 years, Müggelsee has experienced considerable changes in lake catchment and climate. In response to a decrease in external nutrient loading, phytoplankton biomass has declined and its composition has changed (Köhler et al. 2005). Concurrently, higher water temperatures in spring and summer have caused the earlier appearance of various copepods and a prolongation of their period of activity (Gerten and Adrian 2002*b*).

Data

The epilimnetic temperature of Müggelsee was recorded hourly at a depth of 0.5 m in June, July, and August from 1983 to 2002 using an AD590 temperature transducer (Analog Devices, Norwood, Mass.) mounted on a jetty. Daily minimum and maximum epilimnetic temperatures ($T_{0,\mathrm{min}}$ and $T_{0,\mathrm{max}}$, respectively) were extracted from the hourly data. There was a total of 20 gaps in the water temperature data, with a mean duration of 3.5 days and a maximum duration of 6 days. These gaps were filled by linear interpolation. The daily epilimnetic temperature range ($T_{0,\mathrm{dtr}}$) was computed as $T_{0,\mathrm{max}} - T_{0,\mathrm{min}}$. For each year from 1983 to 2002, annual summer means of $T_{0,\mathrm{min}}$, $T_{0,\mathrm{max}}$, and $T_{0,\mathrm{dtr}}$ were computed based on the 92 daily values from 1 June to 31 August. All analyses described below were conducted both on the interpolated data and on the original non-interpolated data. There was no significant difference between the two sets of results; the results presented here are those derived from the interpolated water temperature time series.

Daily meteorological data, covering the same period as the Müggelsee water temperature data, were available from Berlin–Schönefeld Airport (52°23′N, 13°31′E; 46 m a.s.l.), located 10 km southwest of Müggelsee. Data available from this station included daily minimum and daily maximum air temperatures ($T_{\mathrm{air,min}}$ and $T_{\mathrm{air,max}}$, respectively). Hourly mean data on wind speed and relative humidity were also available, from which nighttime (defined as 2000 to 0800) and daytime (0800 to 2000) means were calculated. Cloud cover data were obtained from Berlin–Tempelhof Airport (52°29′N, 13°24′E; 48 m a.s.l.), located 20 km west of Müggelsee. Cloud cover was recorded three times a day (in octals) at 730, 1430, and 2130 CET, and daily mean cloud cover was defined as the arithmetic mean of the three recorded values, converted to a fraction between 0 and 1. The daily air temperature range ($T_{\mathrm{air,dtr}}$) was computed as $T_{\mathrm{air,max}} - T_{\mathrm{air,min}}$. Analogously to water temperature, annual summer means of $T_{\mathrm{air,min}}$, $T_{\mathrm{air,max}}$, and $T_{\mathrm{air,dtr}}$ were computed for each year from 1983 to 2002. No record of any change in observation methods during the study period was found.

In the year 2002, from 1 June to 31 August, water temperature profiles and meteorological data were measured at 5-min intervals at a lake station anchored 300 m from the lakeshore at a depth of 5.5 m. The water temperature profiles were recorded from depths of 0.5 m to 5.0 m using a chain of AD592 temperature transducers (Analog Devices) spaced at intervals of 0.5 m. The meteorological data measured included air temperature, global radiation, wind speed, relative humidity, and air pressure; precipitation was measured simultaneously on the roof of a building located near the lakeshore. The water temperature and meteorological data were aggregated to yield hourly means that were used in the calculation of the heat budget of the lake during summer 2002.

The simultaneous availability of meteorological data measured directly at the lake and at Berlin–Schönefeld Airport from 1 June to 31 August 2002 also allowed the applicability of the airport data to the lake to be assessed. The lake and airport time series were extremely highly correlated, with the proportion of shared variance (r^2) between them being 96% for daily mean air temperature, 92% for daily mean relative humidity, and 83% for daily mean wind speed (with $p < 0.001$ in all cases). The mean difference between the lake and airport time series was 0.2 K for daily mean air temperature, –9.6% for daily mean relative humidity, and –0.6 m·s^{-1} for daily mean wind speed. Thus air temperature at the lake was slightly underestimated by the airport data, whereas relative humidity and wind speed were overestimated. However, this did not affect long-term trends in the data.

The water temperature of the River Spree, by far the most important inflow to Müggelsee, was measured weekly each Monday morning at 1 m depth at the inlet to the lake. The weekly data were interpolated linearly at daily intervals. The rate of inflow to the lake was measured daily at the Freienbrink Monitoring Station, located on the River Spree 13 km upriver from the inlet.

Heat budget model and equilibrium water temperature

The method chosen to analyse the effects of meteorological forcing on the epilimnetic temperature utilised the equilibrium temperature approach of Edinger et al. (1968). This approach is based on a heat budget model in which the net heat flux into a lake, H_{calc} (W·m^{-2}), is computed as the sum of the major heat exchange terms:

$$(1) \qquad H_{calc} = H_S + H_L + H_B + H_E + H_C + H_I + H_P$$

The processes underlying these terms are the absorption of short-wave solar radiation (H_S) and long-wave (infrared) atmospheric radiation (H_L) incident at the lake surface; the emission of long-wave (infrared) radiation from the lake surface (H_B); the exchange of latent heat by evaporation and condensation (H_E); the exchange of sensible heat by convection and conduction (H_C); heat exchange due to mass exchange via the inflow and outflow (H_I); and heat exchange by precipitation directly on to the lake surface (H_P). Heat exchange through the lake bottom is normally considered to be negligible compared with heat exchange across the air–water interface (Ragotzkie 1978).

The short-wave solar radiation absorbed (H_S) is given by

$$(2) \qquad H_S = A_S G$$

where G is the incident global radiation (W·m^{-2}), which is highly dependent on cloud cover (e.g., Kasten and Czeplak 1980), and A_S is an absorption coefficient for short-wave radiation that was set to 0.906 following Kuhn (1978).

The long-wave atmospheric radiation absorbed by the lake (H_L) is given by

$$(3) \qquad H_L + A_L E_L \sigma(T_{air} + 273.15)^4$$

where the absorption coefficient A_L of the water for long-wave radiation was set to 0.97 (Anderson 1954), σ is the Stefan–Boltzmann constant (56.7×10^{-9} W·m^{-2}·K^{-4}), T_{air} is the air temperature (°C), and E_L is the emission coefficient of the atmosphere. Using the formula of Brutsaert (1982), this latter is given by

$$(4) \qquad E_L = 1.24[e_a/(T_{air} + 273.15)]^{1/7}(1 + 0.17C^2)$$

where e_a is the water vapour pressure (hPa), given by the product of the saturation vapour pressure e_s (hPa) and the relative humidity r_h (%):

$$(5) \qquad e_a = e_s r_h/100$$

where e_s was obtained from the Magnus formula (Murray 1967):

$$(6) \qquad e_s = 6.1078 \exp[(17.2694\, T_{air})/(237.36 + T_{air})]$$

and C is the degree of cloud cover (ranging from 0 to 1). C was estimated empirically from the ratio of incident global radiation (G) to clear-skies global radiation (G_0) using the following equation of Kasten and Czeplak (1980):

$$(7) \qquad G/G_0 = 1 - aC^b$$

with $a = 0.72$ and $b = 3.2$, values that are considered to be representative for Germany (Kasten et al. 1984). The degree of cloud cover during nighttime was estimated by linear interpolation of daytime values.

The emission of long-wave radiation from the lake surface (H_B) proceeds according to the Stefan–Boltzmann law with an emission coefficient of 0.97:

$$(8) \qquad H_B = -0.97\,\sigma(T_0 + 273.15)^4$$

where T_0 is the surface water temperature (°C).

The loss of latent heat by evaporation from the lake surface (H_E) is influenced by wind speed:

$$(9) \qquad H_E = -f(e_s - e_a)$$

where f is the wind function (W·m^{-1}·hPa^{-1}), here given by modifying the wind function of McMillan as cited by Sweers (1976) by including an air stability term (Dingman 1972) to yield the following equation as used by Kuhn (1978) and by Livingstone and Imboden (1989):

$$(10) \qquad f = 4.4 + 1.82u_{10} + 0.26(T_0 - T_{air})$$

where u_{10} is the wind speed 10 m above the lake surface (m·s^{-1}). Assuming a logarithmic wind speed profile, the wind speed at the standard meteorological height of 10 m was estimated to be 8% greater than the actual measured wind speed 4 m above the lake surface.

The convective exchange of sensible heat (H_C) is also dependent on wind speed:

$$(11) \qquad H_C = -Rf(T_0 - T_{air})$$

where R is the Bowen coefficient (Bowen 1926), dependent on air pressure, which relates H_C to H_E.

The heat exchange due to the inflow and outflow (H_I) is given by

$$(12) \qquad H_I = Qc_p\rho(T_{inflow} - T_0)/A_0$$

where Q is the lake discharge (m^3·s^{-1}), c_p is the specific heat of water at constant pressure (4200 J·kg^{-1}·K^{-1}), ρ is the density of water (1000 kg·m^{-3}), T_{inflow} is the mean inflow temperature (°C), and A_0 is the lake surface area (7.3×10^6 m^2 for Müggelsee).

The effect of direct precipitation on the lake surface (H_P) on the heat flux of the lake is given by

$$(13) \qquad H_P = Pc_p\rho(T_{air} - T_0)$$

where P is the precipitation rate (m·s^{-1}).

The model was verified by comparing the net heat flux calculated from the meteorological data (H_{calc}) with the net heat flux calculated directly from the measured lake temperature data (H_{meas}), given by

$$(14) \qquad H_{meas} = \mathrm{d}E/\mathrm{d}t$$

where E is the heat content of the lake per unit area. Assuming constant values for c_p and ρ, E was obtained as follows by integration of the hourly volume-weighted temperature profiles:

$$(15) \quad E = (c_p \rho / A_0) \int_0^{z_m} T_z A_z \, \mathrm{d}z$$

where T_z and A_z are the temperature and isobath area, respectively, at depth z, and z_m is the maximum lake depth.

The equilibrium temperature T_{eq} of Edinger et al. (1968), defined as the surface temperature that would result in zero net heat flux, is the temperature that theoretically would ultimately be reached by the water surface under stationary environmental conditions. T_{eq} is computed by setting $H_{calc} = 0$ and solving eq. 1 for $T_{eq} = T_0$. T_{eq} continually changes in response to variations in meteorological forcing; simultaneously, T_0 is continually being driven exponentially toward T_{eq} by the difference between the two. Under ordinary circumstances, T_0 will cross T_{eq} twice per day, as warming and cooling trends alternate in response to the diurnal cycle (Edinger et al. 1968). A further characteristic of the response of water temperature to meteorological forcing is the time lag that exists between the occurrence of the daily maximum equilibrium temperature and the occurrence of the daily maximum water temperature, which may approach a maximum of 6 h for the diel cycle (Edinger et al. 1968). T_{eq} exhibits a much larger diel amplitude than does the lake water surface temperature T_0, mainly owing to the strong diel variation in H_S and H_E (Edinger et al. 1968; Marti and Imboden 1986).

Exponential smoothing

Based on the example of lakes in Greenland, Kettle et al. (2004) introduced a method of modelling lake surface water temperature empirically based on the exponential filtering of ambient air temperature. As shown by Kettle et al. (2004), this approach is interpretable physically in terms of a sensible heat exchange model (e.g., Rodhe 1952; Billelo 1964), where the rate of change of T_0 with time is driven by the difference between T_{air} and T_0 and is proportional to this difference. The governing differential equation is that of Newton's law of cooling:

$$(16) \quad \mathrm{d}T_0/\mathrm{d}t = k(T_{air} - T_0)$$

Assuming T_{air} to be approximately constant, the solution to eq. 16 can be written as follows:

$$(17) \quad \begin{aligned} T_0(t) &= T_{air}(t) + [T_0(0) - T_{air}(t)]\mathrm{e}^{-kt} \\ &= \mathrm{e}^{-kt} T_0(0) + [1 - \mathrm{e}^{-kt}]T_{air}(t) \end{aligned}$$

showing that T_0 follows T_{air} exponentially. Over a small time-step δt from $t - \delta t$ to t, it follows that

$$(18) \quad T_0(t) = \mathrm{e}^{-k\delta t} T_0(t - \delta t) + [1 - \mathrm{e}^{-k\delta t}]T_{air}(t)$$

Setting $\alpha = 1 - e^{-k\delta t}$ yields the difference equation for an exponential filter, where α is the exponential smoothing coefficient:

$$(19) \quad T_0(t) = (1 - \alpha)T_0(t - \delta t) + \alpha T_{air}(t)$$

Thus the sensible heat exchange model described by differential eq. 16 is mathematically equivalent to applying exponential smoothing to the ambient air temperature. The smoothing coefficient α, which is dependent on the sampling interval δt, is confined to the interval [0,1], with smoothing being absent at $\alpha = 1$ and increasing to a maximum as $\alpha \rightarrow 0$. Exponential filtering reduces the variance of a time series and introduces a time delay. The approach of Kettle et al. (2004), i.e., eq. 19, has been used successfully to model the surface temperature of mountain lakes in the Swiss Alps (Livingstone et al. 2005) and the Tatras (Šporka et al. 2006) based on air temperature alone, although Kettle et al. (2004) also included clear-sky solar radiation in their original model.

To take account of meteorological driving variables other than just air temperature, the same approach can be applied to the equilibrium temperature, as the rate at which T_0 is driven towards T_{eq} is proportional to $T_{eq} - T_0$, which results in T_0 tending towards T_{eq} exponentially (e.g., Edinger et al. 1968; Sweers 1976; Livingstone and Imboden 1989):

$$(20) \quad \mathrm{d}T_0/\mathrm{d}t = k(T_{eq} - T_0)$$

Replacing T_{air} by T_{eq} in eqs. 17–19, it follows that differential eq. 20 is equivalent to applying exponential smoothing to the equilibrium temperature:

$$(21) \quad T_0(t) = (1 - \alpha)T_0(t - \delta t) + \alpha T_{eq}(t)$$

Viewed purely empirically, double exponential smoothing (i.e., smoothing the exponentially smoothed data a second time) would be more suited to time series in which a trend is present, Holt–Winters smoothing would cope better with periodic data, and a combination of both techniques would cope best with time series that contain both a trend and a periodic component. However, the advantages of the physical interpretability of eqs. 19 and 21 outweigh any empirical advantage that might be conferred by full double exponential Holt–Winters smoothing (which also requires two additional smoothing parameters). In the following, we use eqs. 19 and 21 with $\delta t = 1$ h to model lake surface temperature not only in terms of the air temperature T_{air} alone, but also in terms of the equilibrium temperature T_{eq}.

Results

Long-term changes in daily air and water temperature extrema and ranges

For the 20-year period 1983–2002, we illustrate a comparison of the time series of the summer means of $T_{0,min}$ and $T_{0,max}$ (Fig. 1*a*) with the summer means of $T_{air,min}$ and $T_{air,max}$ (Fig. 1*b*). Although the four time series exhibit similarities in their temporal structure, there are also substantial differences in behaviour, especially in the long term. To test for the presence of linear trends in these non-normally distributed time series, the Theil–Sen trend, defined as the median of all possible slopes between the data points, taken pairwise (Theil 1950; Sen 1968), was computed and tested for statistical significance at the $p < 0.1$ level using the nonparametric Kendall tau statistic (Helsel and Hirsch 1992). A significant increasing trend was confirmed in both $T_{0,min}$ and $T_{air,min}$, but not in either $T_{0,max}$ or $T_{air,max}$ (Table 1). The long-term changes in daily water and air temperature extrema described above are reflected in the corresponding daily temperature ranges (Figs. 1*c*, 1*d*). Although the daily air

Fig. 1. Summer (June–August) means of (*a*) daily minimum epilimnetic temperature ($T_{0,min}$, ☐) and daily maximum epilimnetic temperature ($T_{0,max}$, ●), (*b*) daily minimum air temperature ($T_{air,min}$, ☐) and daily maximum air temperature ($T_{air,max}$, ●), (*c*) daily epilimnetic temperature range ($T_{0,dtr} = T_{0,max} - T_{0,min}$) and (*d*) daily air temperature range ($T_{air,dtr} = T_{air,max} - T_{air,min}$) for Müggelsee from 1983 to 2002.

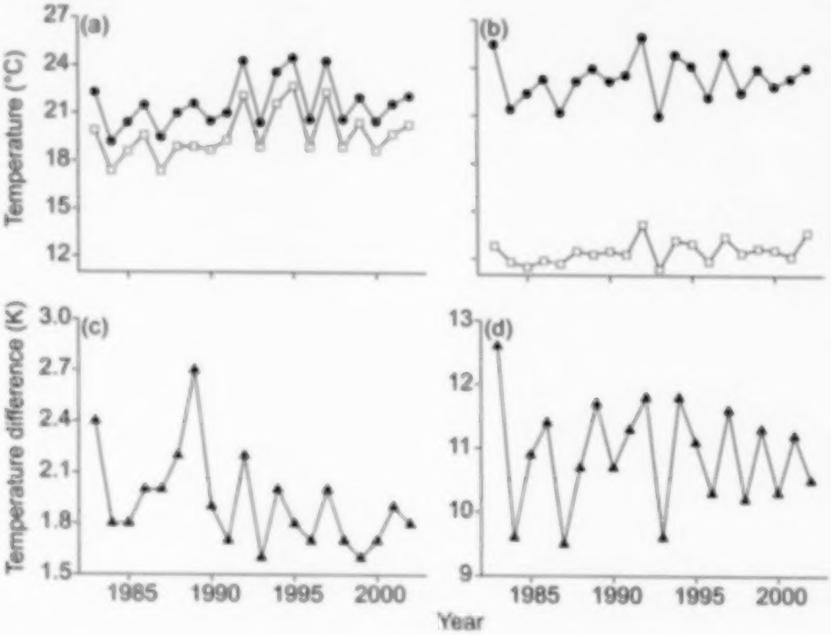


Table 1. Statistics of the epilimnetic temperature of Müggelsee and of the air temperature at Berlin–Schönefeld Airport, 10 km from Müggelsee.

	Overall median temperature (°C)	Median absolute deviation (K)	Theil–Sen trend (K·year^{-1})	*p*
$T_{0,min}$	19.1	0.5	0.083	0.06
$T_{0,max}$	21.3	0.8	0.069	ns
$T_{0,dtr}$	1.9	0.2	–0.016	0.05
$T_{air,min}$	12.4	0.5	0.054	0.08
$T_{air,max}$	23.4	0.8	0.054	ns
$T_{air,dtr}$	11.0	0.6	–0.015	ns

Note: $T_{0,min}$, mean summer daily minimum epilimnetic temperature; $T_{0,max}$, mean summer daily maximum epilimnetic temperature; $T_{0,dtr}$, mean summer daily epilimnetic temperature range (= $T_{0,max} - T_{0,min}$); $T_{air,min}$, $T_{air,max}$, $T_{air,dtr}$, analogous values for air temperature. Summer was defined as 1 June – 31 August and the period covered was 1983 to 2002. Significance levels (*p*) of the Theil–Sen trend were calculated from the Kendall tau statistic (ns, not significant at the $p < 0.1$ level).

temperature range ($T_{air,dtr}$) exhibited no detectable long-term trend, the daily epilimnetic temperature range ($T_{0,dtr}$) showed a distinct decreasing trend ($p = 0.05$) (Table 1). In all cases, the Theil–Sen trends in the water temperature time series were stronger than those in the corresponding air temperature time series (Table 1).

Heat budget model and equilibrium water temperature

The calculated overall mean net heat flux into the lake (H_{calc}) during summer 2002 was 6.9 W·m^{-2}. An analysis of the individual heat flux terms contributing to H_{calc} (Fig. 2*a*) confirmed that in Müggelsee, as in other lakes, the emission and absorption of long-wave radiation at the lake surface are the most important processes involved, with H_B (–413.7 W·m^{-2}) having the highest magnitude and H_L (354.2 W·m^{-2}) having the second highest. H_S (180.9 W·m^{-2}) and H_E (–96.4 W·m^{-2}) were also important terms, with H_S being the most important forcing term during the daylight hours. The contribution of H_C (–15.9 W·m^{-2}) was relatively minor, and that of H_F (–1.7 W·m^{-2}) was negligible. The heat flux H_P due to precipitation was the least important on average (–0.7 W·m^{-2}), but decreased to as low as –102 W·m^{-2} during individual precipitation events. Thus H_P can be relevant to the lake heat budget in the short term.

A comparison of calculated and measured heat fluxes revealed that although the amplitude of the diel variation in

Fig. 2. Time series of the heat flux into Müggelsee during summer 2002: (*a*) 24-h moving averages of the individual heat flux terms of eq. 1 (note that the very small terms H_I and H_P are not shown as they would be indistinguishable from zero on this plot); (*b*) comparison of 5-day moving averages of the net heat flux calculated from eq. 1 (H_calc, solid line) with 5-day moving averages of the net heat flux obtained from temperature profile measurements (H_meas, dotted line).

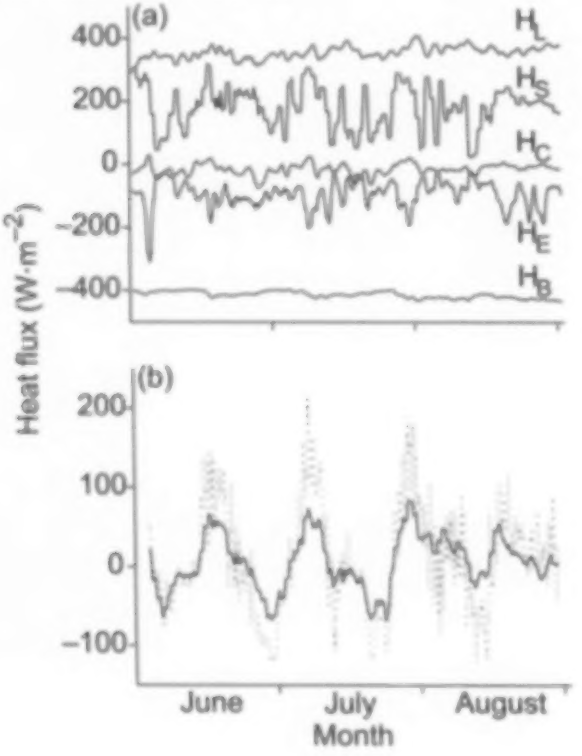
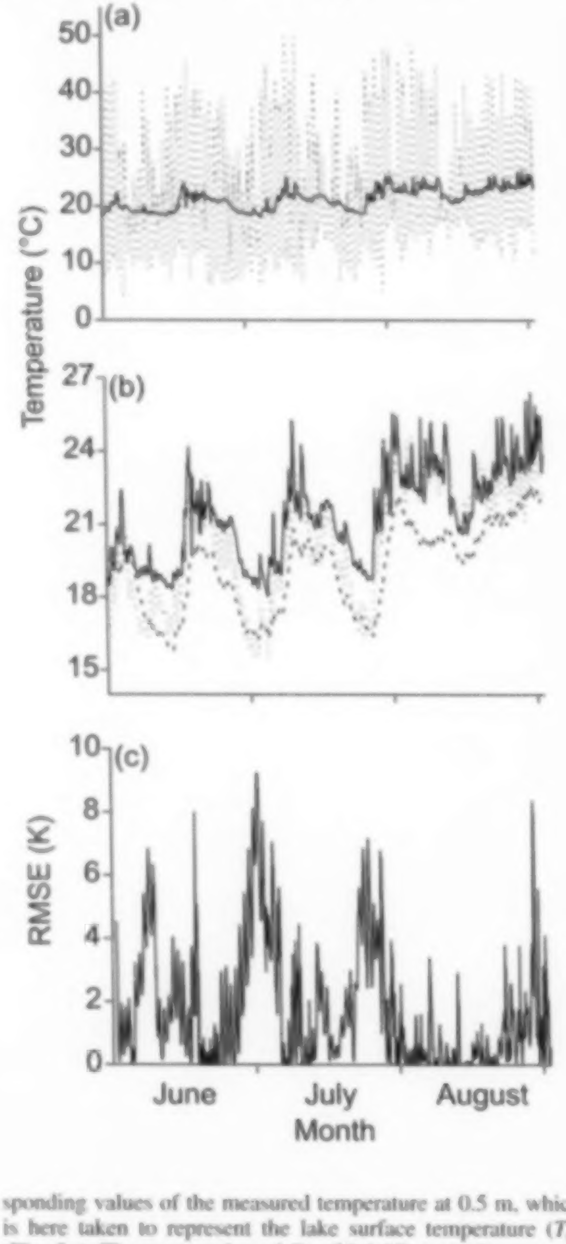


Fig. 3. Comparison of the measured epilimnetic temperature of Müggelsee (T_0) with the air temperature measured at Berlin–Schönefeld Airport (T_air) and with the calculated equilibrium temperature of the lake surface (T_eq) during summer 2002: (*a*) comparison of unsmoothed hourly values of T_0 (solid line) and T_eq (dotted line); (*b*) comparison of hourly values of T_0 (solid line) with hourly values of T_air (broken line) and T_eq (dotted line) smoothed using eqs. 19 and 21; (*c*) the root mean square error (RMSE) between T_0 and T_eq (smoothed).



H_meas was not well accounted for by H_calc, averaging over several days drastically reduced the discrepancy between the two time series, so that H_calc provided a good estimate of longer-period temporal variations in H_meas (Fig. 2*b*). Discrepancies between H_meas and H_calc at higher frequencies are likely to be irrelevant, as the high-frequency variability of H_meas is almost certain to be predominantly an artefact due to seiching. When stratified, Müggelsee exhibits basin-wide circulation in response to wind pulses that set up internal seiches, thus causing local variations in the depth of the thermocline (Lorke 1998). This process can produce huge, rapid changes in H_meas, which depends on temperature profiles measured at only one location in the lake, that do not in fact reflect the situation pertaining in the water body as a whole. This interpretation is supported by the results of a comparison of H_meas during periods of stratification (when seiching can occur) with H_meas during periods of homothermy (when seiching cannot occur), which revealed that the variability of H_meas was much higher during the former than during the latter.

Hourly values of the equilibrium temperature (T_eq) calculated from the heat budget model are compared with corresponding values of the measured temperature at 0.5 m, which is here taken to represent the lake surface temperature (T_0) (Fig. 3*a*). The mean value of T_eq (20.6 °C) agreed very well with that of T_0 (21.3 °C). The amplitudes of the diel cycles of T_0 and T_eq, however, were vastly different, with that of T_eq

(mean value of 12.9 K) exceeding that of T_0 (0.7 K) by a factor of about 18 (Fig. 3*a*). This agrees with the theoretical conclusions of Edinger et al. (1968), who showed that the diel amplitude of T_0, which is driven by T_{eq}, could be only a small proportion of the diel amplitude of T_{eq} itself.

The exponential smoothing approach of Kettle et al. (2004) was used to model T_0 empirically based on air temperature (T_{air}) alone using eq. 19 with δt = 1 h. An optimum value of the smoothing coefficient α was determined by minimising the root mean square error (RMSE) between the measured and modelled time series of T_0. The optimum fit was found for α = 0.010, yielding an overall RMSE of 2.7 K. The model successfully reproduced the main features of the temporal structure of T_0, although the modelled values were consistently somewhat low (on average, 2.2 K) and the high-frequency variability was suppressed (Fig. 3*b*). The exchange coefficient $k = -[\ln(1 - \alpha)]/\delta t$ corresponding to α = 0.010 and δt = 1 h is 0.24 day^{-1}, which agrees well with the value of k corresponding to the mean value of α found by Kettle et al. (2004) for lakes in southwest Greenland (α = 0.23, δt = 1 day, k = 0.26 day^{-1}).

An analogous approach was then employed to model T_0 based on T_{eq} instead of T_{air}, using eq. 21 with δt = 1 h. Because T_{eq} incorporates the forcing effects not only of air temperature, but also of the other relevant meteorological variables (mainly wind speed, relative humidity, and cloud cover), eq. 21 should yield a better simulation of T_0 than eq. 19. This was indeed found to be the case; the optimum value found for the smoothing coefficient (α = 0.015, i.e., k = 0.36 day^{-1}) yielded an RMSE of 0.9 K, substantially better than the value obtained using T_{air}. The model successfully reproduced not only the main features of the temporal structure of T_0, but much of its high-frequency structure as well (Fig. 3*b*). The superiority of an approach based on smoothing T_{eq} rather than T_{air} is most obvious in the later part of the summer (Fig. 3*b*), when the RMSE was generally very low (Fig. 3*c*). Comparing the ability of eqs. 19 and 21 to reproduce the measured values of $T_{0,min}$, $T_{0,max}$, and $T_{0,dtr}$ (Table 2), it again emerges that the approach based on T_{eq} (eq. 21) is superior to that based on T_{air} (eq. 19), with consistently lower RMSE values in all cases. The simulation of $T_{0,dtr}$, with an RMSE of only 0.3 K, was exceptionally good. A linear regression of $T_{0,min}$ on $T_{air,min}$ after smoothing, and of $T_{0,max}$ on $T_{air,max}$ after smoothing, yielded r^2 values of 0.82 and 0.76, respectively. The corresponding r^2 values for linear regressions based on $T_{eq,min}$ and $T_{eq,max}$ after smoothing, 0.88 in both cases, were distinctly higher. A linear regression of the daily temperature range $T_{0,dtr}$ on $T_{eq,dtr}$ after smoothing (r^2 = 0.52) also yielded better results than a linear regression of $T_{0,dtr}$ on $T_{air,dtr}$ after smoothing (r^2 = 0.26). This clearly demonstrates the improvement in fit achieved by basing the model on T_{eq} rather than T_{air}.

Table 2. Root mean square errors (RMSE) between observed values of $T_{0,min}$ and smoothed values of $T_{air,min}$ and $T_{eq,min}$; between observed values of $T_{0,max}$ and smoothed values of $T_{air,max}$ and $T_{eq,max}$; and between observed values of $T_{0,dtr}$ and smoothed values of $T_{air,dtr}$ and $T_{eq,dtr}$ for summer 2002.

	RMSE (K)	
	T_{air}	T_{eq}
$T_{0,min}$	1.8	1.1
$T_{0,max}$	4.0	0.8
$T_{0,dtr}$	0.8	0.3

Note: Smoothing was accomplished by using eq. 19 with α = 0.010 for T_{air} and eq. 21 with α = 0.015 for T_{eq}. $T_{0,min}$, mean summer daily minimum epilimnetic temperature; $T_{0,max}$, mean summer daily maximum epilimnetic temperature; $T_{0,dtr}$, mean summer daily epilimnetic temperature range (= $T_{0,max} - T_{0,min}$); T_{air}, T_{eq}, analogous values for air temperature and equilibrium temperatures, respectively.

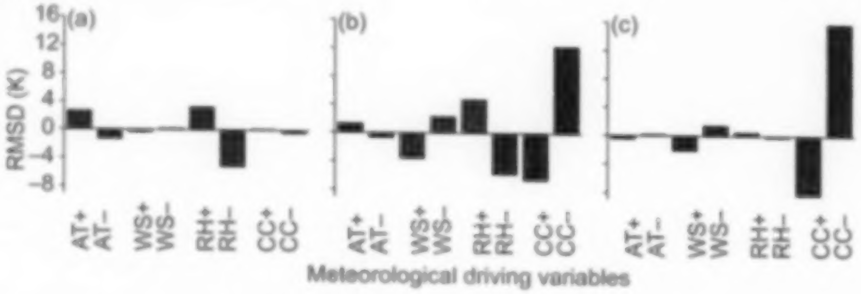
Modelling the effect of the meteorological driving variables on the daily water temperature extrema

The heat exchange processes described by eqs. 1–13 are dependent on very few driving variables. In addition to clear-sky solar radiation, which is essentially a predetermined astronomical variable, the most important of these are air temperature, wind speed, relative humidity, and cloud cover (e.g., Edinger et al. 1968; Sweers 1976; Livingstone and Imboden 1989). Because T_0 is determined predominantly by T_{eq}, a sensitivity analysis based on the heat budget model can be used to determine the relative influence of these driving variables on the daily extrema of T_{eq}, and hence on $T_{0,min}$ and $T_{0,max}$. This was done by calculating T_{eq} based not only on the hourly measured meteorological data, but also on the values that result when these data are decreased and increased by amounts corresponding to the lower and upper quartiles of each input data set, respectively. For each of the hourly time series of air temperature, wind speed, relative humidity, and cloud cover from 1 June to 31 August 2002, the median and the upper and lower quartiles were calculated. For each of the four time series, two new time series were created by decreasing each hourly value in the original time series by the difference between the median and the lower quartile and by increasing each hourly value in the original time series by the difference between the upper quartile and the median. This allowed the effect on T_{eq} of lowering or raising each of the four variables by one quartile to be determined. This non-parametric approach made it unnecessary to make any assumptions about the form of the probability distributions of the driving variables.

An increase (decrease) in either air temperature or relative humidity resulted in an increase (decrease) in both $T_{eq,min}$ (Fig. 4*a*) and $T_{eq,max}$ (Fig. 4*b*). Although an increase (decrease) in either wind speed or cloud cover resulted in a decrease (increase) in $T_{eq,max}$ (Fig. 4*b*), variations in these two driving variables had essentially no effect on $T_{eq,min}$ (Fig. 4*a*). $T_{eq,min}$ reacted most sensitively to variations in relative humidity and air temperature, whereas $T_{eq,max}$ reacted most sensitively to changes in cloud cover and relative humidity.

The effect of variations in the four meteorological driving variables differed between nighttime ($T_{eq,min}$) and daytime ($T_{eq,max}$) (Figs. 4*a*, 4*b*). This day–night asymmetry in the effects of each meteorological driving variable resulted in corresponding increases or decreases in $T_{eq,dtr}$ (Fig. 4*c*). Increases (decreases) in either wind speed or cloud cover resulted in corresponding decreases (increases), in $T_{eq,dtr}$, which were substantial in the case of cloud cover. The effect of

Fig. 4. The root mean square deviation (RMSD) between the equilibrium temperature of the surface of Müggelsee during summer 2002 calculated (*i*) from measured meteorological data and (*ii*) by increasing (+) and decreasing (–) the meteorological driving variables air temperature (AT), wind speed (WS), relative humidity (RH), and cloud cover (CC) by amounts corresponding to the upper and lower quartiles of the data measured during the period 1983–2002. (*a*) RMSD for the daily minimum equilibrium temperature ($T_{\mathrm{eq,min}}$). (*b*) RMSD for the daily maximum equilibrium temperature ($T_{\mathrm{eq,max}}$). (*c*) RMSD for the daily equilibrium temperature range ($T_{\mathrm{eq,dtr}} = T_{\mathrm{eq,max}} - T_{\mathrm{eq,min}}$).



variations in air temperature and relative humidity on $T_{\mathrm{eq,dtr}}$ was comparatively slight.

During the period 1983–2002, the summer means of air temperature, wind speed, relative humidity, and cloud cover varied within the ranges 16.2–20.4 °C, 3.0–3.9 m·s^{-1}, 62.1%–76.6%, and 46.9%–64.0%, respectively. Although there was no obvious long-term change in either air temperature or relative humidity, both wind speed and cloud cover appeared to undergo a slight long-term increase. However, given the high degree of interannual variability, these apparent long-term increases were not statistically significant and, therefore, in themselves do not offer a convincing explanation for the long-term changes in $T_{0,\mathrm{min}}$ and hence in $T_{0,\mathrm{dtr}}$.

To investigate the causes and consequences of the long-term increase in $T_{0,\mathrm{min}}$ in more detail, nighttime and daytime estimates of the most important meteorologically dependent heat flux terms were computed from eqs. 2–11 for each day of each summer from 1983 to 2002. During both night and day, H_{I} and H_{P} were assumed to be negligible. During the night, H_{S} was assumed to be zero. Nighttime estimates of H_{L}, H_{B}, H_{E}, and H_{C} were computed from $T_{\mathrm{air,min}}$, $T_{0,\mathrm{min}}$, C (daily mean), u_{10} (nighttime mean), and r_{h} (nighttime mean); daytime estimates of H_{L}, H_{B}, H_{S}, H_{E}, and H_{C} were computed from $T_{\mathrm{air,max}}$, $T_{0,\mathrm{max}}$, C (daily mean), u_{10} (daytime mean), and r_{h} (daytime mean). The lack of data on cloud cover during the night necessitated the use of the daily mean cloud cover (actually a daytime mean) to compute both nighttime and daytime estimates. For both nighttime and daytime, the estimates were then averaged to provide separate estimates of the nighttime and daytime heat flux terms for each summer from 1983 to 2002. The respective Theil–Sen trends were then computed and tested for significance using the Kendall tau test as before (Table 3).

Of the five major components of the heat flux, two (H_{S} and H_{E}) exhibited no significant long-term trend in either their nighttime or daytime estimates. Terms H_{B} and H_{C} exhibited no significant long-term trend in their daytime estimates, but did exhibit significant decreasing trends in their nighttime estimates. Finally, both the daytime and nighttime estimates of H_{L} exhibited a significant increasing trend, with the nighttime trend exceeding the daytime trend by 37%.

The long-term behaviour of the heat flux terms can be explained in terms of the relevant driving variables. The only driving variables to exhibit a statistically significant long-term trend are $T_{0,\mathrm{min}}$ and $T_{\mathrm{air,min}}$. During the night, a long-term increase in lake surface water temperature automatically results in the increased emission of long-wave radiation from the lake surface (eq. 8), causing a long-term decrease in H_{B}. The long-term increase in $T_{0,\mathrm{min}}$ exceeds that in $T_{\mathrm{air,min}}$ by 54% (Table 1); this difference in trend suffices to induce a long-term increase in nighttime convective heat loss (eq. 11), i.e., a long-term decrease in H_{C}. The emission of long-wave radiation from the atmosphere (H_{L}) is a comparatively complex process that is driven by air temperature, relative humidity, and cloud cover. Taken individually, none of these driving variables exhibits a significant long-term daytime trend; taken together, however, the long-term changes in all three variables do yield a statistically significant long-term increase in daytime H_{L} (Table 3). Given the significant increasing trend in $T_{\mathrm{air,min}}$, the long-term increase in nighttime H_{L} is not only much more highly significant than that in daytime H_{L}, but is also 37% greater in magnitude (Table 3). The main process responsible for the significant long-term increase in $T_{0,\mathrm{min}}$ is therefore the emission of long-wave radiation from the atmosphere. Looking at this process in more detail, during the night a significant long-term increase is detected not only in $T_{\mathrm{air,min}}$ (and in the factor $\sigma\,(T_{\mathrm{air,min}} + 273.15)^4 = \mathrm{SB}_{\mathrm{L}}$), but also in the factor E_{L}, the emission coefficient of the atmosphere (Table 3). From eqs. 4–6, an increase in E_{L} can result because of the increase in e_{s}, and hence in e_{a}, that would result from an increase in $T_{\mathrm{air,min}}$. However, it can also result from an increase in e_{a} associated with an increase in relative humidity, or from an increase in cloud cover. However, the lack of a statistically significant trend in either of the latter two meteorological variables suggests that the long-term increase in the nighttime values of E_{L} are also predominantly the result of the long-term increase in $T_{\mathrm{air,min}}$.

Discussion

An asymmetric increase in the daily air temperature extrema, leading to a decrease in the daily air temperature range, has characterized recent climate warming throughout the Northern Hemisphere (e.g., Karl et al. 1993). Our study demonstrates for the first time that an analogous phenome-

Table 3. Statistics of meteorological driving variables and corresponding estimates of the nighttime and daytime heat flux terms into Müggelsee during summer.

	Overall median value	Median absolute deviation	Theil–Sen trend	p
Nighttime				
u_{10}	3.0 $m\cdot s^{-1}$	0.2 $m\cdot s^{-1}$	0.018 $m\cdot s^{-1}\cdot year^{-1}$	ns
r_h	77.6%	3.4%	0.204%$\cdot year^{-1}$	ns
H_L	305.8 $W\cdot m^{-2}$	3.0 $W\cdot m^{-2}$	0.512 $W\cdot m^{-2}\cdot year^{-1}$	0.004
E_L	0.83	0.01	0.001 $year^{-1}$	0.06
SB_L	377.1 $W\cdot m^{-2}$	2.8 $W\cdot m^{-2}$	0.288 $W\cdot m^{-2}\cdot year^{-1}$	0.08
H_B	–401.5 $W\cdot m^{-2}$	3.0 $W\cdot m^{-2}$	–0.458 $W\cdot m^{-2}\cdot year^{-1}$	0.04
H_E	–37.3 $W\cdot m^{-2}$	6.7 $W\cdot m^{-2}$	0.032 $W\cdot m^{-2}\cdot year^{-1}$	ns
H_C	–52.3 $W\cdot m^{-2}$	5.4 $W\cdot m^{-2}$	–0.563 $W\cdot m^{-2}\cdot year^{-1}$	0.05
Daytime				
u_{10}	4.0 $m\cdot s^{-1}$	0.2 $m\cdot s^{-1}$	0.012 $m\cdot s^{-1}\cdot year^{-1}$	ns
r_h	63.6%	3.1%	–0.105%$\cdot year^{-1}$	ns
C	58.9%	4.1%	0.172%$\cdot year^{-1}$	ns
H_S	182.5 $W\cdot m^{-2}$	6.5 $W\cdot m^{-2}$	0.064 $W\cdot m^{-2}\cdot year^{-1}$	ns
H_L	376.7 $W\cdot m^{-2}$	2.8 $W\cdot m^{-2}$	0.373 $W\cdot m^{-2}\cdot year^{-1}$	0.04
E_L	0.89	0.01	0.000 $year^{-1}$	ns
SB_L	438.2 $W\cdot m^{-2}$	4.9 $W\cdot m^{-2}$	0.317 $W\cdot m^{-2}\cdot year^{-1}$	ns
H_B	–413.5 $W\cdot m^{-2}$	4.6 $W\cdot m^{-2}$	–0.406 $W\cdot m^{-2}\cdot year^{-1}$	ns
H_E	–114.6 $W\cdot m^{-2}$	18.1 $W\cdot m^{-2}$	–0.431 $W\cdot m^{-2}\cdot year^{-1}$	ns
H_C	12.1 $W\cdot m^{-2}$	3.2 $W\cdot m^{-2}$	–0.226 $W\cdot m^{-2}\cdot year^{-1}$	ns

Note: The equivalent statistics of the epilimnetic temperature of Müggelsee (T_0) and of the air temperature at Berlin–Schönefeld Airport (T_{air}) are listed in Table 1. u_{10}, wind speed at Berlin–Schönefeld Airport; r_h, relative humidity at Berlin–Schönefeld Airport; C, cloud cover at Berlin–Tempelhof Airport; H_S, heat flux due to absorption of short-wave (solar) radiation; H_L, heat flux due to absorption of long-wave (atmospheric) radiation; E_L, emission coefficient of the atmosphere; $SB_L = \sigma(T_{air} + 273.15)^4$, heat flux emitted from a black body by Stefan–Boltzmann radiation (eq. 3); H_B, heat flux due to the emission of long-wave radiation from the lake surface; H_E, heat flux due to latent heat exchange; H_C, heat flux due to convective heat exchange. Summer was defined as 1 June – 31 August and the period covered was 1983 to 2002. Significance levels (p) of the Theil–Sen trend were calculated from the Kendall tau statistic (ns, not significant at the $p < 0.1$ level). The units of the Theil–Sen trend are the respective units of the variable concerned per year.

non can be detected in lake epilimnetic temperatures. During summer, from 1983 to 2002, $T_{0,min}$ in Müggelsee increased more rapidly than $T_{0,max}$, resulting in a distinct decrease in $T_{0,dtr}$. However, the decrease in $T_{0,dtr}$ cannot be explained simply in terms of a response to $T_{air,dtr}$, which in fact remained essentially constant during the study period.

Various studies have shown that daily minimum air temperatures have generally been rising faster than daily maximum air temperatures not only globally (e.g., Easterling et al. 1997), but also in central Europe (e.g., Wibig and Glowicki 2002), including Germany (Heino et al. 1999). This is not always the case, however: according to Brázdil et al. (1996), the daily air temperature range in central Europe changed very little between 1951 and 1990. In agreement with this, we found that both $T_{air,min}$ and $T_{air,max}$ in Berlin rose by ~0.05 K·year^{-1} during our 1983–2002 study period, resulting in essentially no long-term change in $T_{air,dtr}$. Air temperature is arguably the most important of the meteorological variables driving T_{eq}, and hence T_0, as it is involved in most daily heat exchange processes (e.g., Edinger et al. 1968). However, substantial discrepancies with respect to both fluctuations and long-term trends exist between $T_{0,min}$ and $T_{air,min}$ and between $T_{0,max}$ and $T_{air,max}$. These discrepancies lead to even more pronounced discrepancies between $T_{0,dtr}$ and $T_{air,dtr}$. Thus the asymmetric increase in $T_{0,min}$ and $T_{0,max}$ is unlikely to be interpretable in terms of air temperature alone; the influence of other meteorological driving variables must also be taken into account.

In addition to air temperature, the most important meteorological driving variables involved in determining the lake heat budget, and thus T_{eq} and T_0, are wind speed, relative humidity, and cloud cover (e.g., Edinger et al. 1968). The good fit between measured values of T_0 and exponentially smoothed values of T_{eq} indicates that an analysis of the sensitivity of $T_{eq,min}$ and $T_{eq,max}$ to variations in these driving variables can be interpreted to show their relative influence on $T_{0,min}$ and $T_{0,max}$. The results of the sensitivity analysis demonstrate that each of the four meteorological driving variables has a perceptible effect on one or both of $T_{eq,min}$ and $T_{eq,max}$. The pronounced effects of relative humidity and cloud cover on the magnitude of T_{eq} agree with the results of Marti and Imboden (1986) and Livingstone and Imboden (1989), who showed the strong dependence of the net heat flux on these variables.

The effects of the meteorological driving variables on $T_{eq,min}$ and $T_{eq,max}$ are not only substantial, but also asymmetric. The greatest degree of day–night asymmetry in the effects of these variables was exhibited by cloud cover and, to a lesser extent, wind speed, suggesting that these two variables may have contributed substantially to the diel asymmetry in T_{eq} and hence to the discrepancy between $T_{0,\mathrm{dir}}$ and $T_{\mathrm{air,dir}}$. Because of the non-linearities inherent in the equations describing the heat flux terms, fluctuations in the daily means of the driving variables can therefore induce a degree of day–night asymmetry in T_{eq}, and hence in T_0, without day–night asymmetry necessarily having to be present in the driving variables themselves.

The presence of day–night asymmetry in the driving variables themselves makes the situation more complex. Computation of nighttime and daytime estimates of the individual heat flux components based on a coarse day–night separation of the driving variables revealed significant long-term increases in nighttime heat loss from the lake due to the emission of infrared radiation from the lake surface and to convective processes in the atmospheric boundary layer above the lake surface, which in both cases can be confidently traced back to the observed long-term increase in epilimnetic temperature. These processes are essentially negative feedback processes that automatically regulate lake temperatures, preventing them from increasing steeply when subjected to increasing heat input (e.g., Peeters et al. 2002). This increasing heat input can only result from increases in incident radiation, either short-wave (H_S) or long-wave (H_L), both of which generally account for a very high proportion of the incoming heat flux. An increase in incident short-wave (solar) radiation can be ruled out not only because it exhibits no significant long-term trend during the study period, but also because any increase in incident solar radiation would clearly affect daily maximum (daytime) water temperatures much more strongly than daily minimum (nighttime) temperatures. This leaves the long-term increase in incident long-term atmospheric radiation as the only likely root cause of the overall long-term gross increase in heat input. Not only is H_L the only component of the heat balance to exhibit a statistically significant increasing long-term trend, but this trend is also substantially steeper during nighttime than during daytime. Although H_L is the most difficult of all the major heat flux terms to parameterize (Edinger et al. 1968), it is clear that air temperature, relative humidity, and cloud cover are the major meteorological variables that determine it. The only relevant meteorological driving variable with a statistically significant increasing nighttime trend is air temperature, which has both a direct effect on H_L via Stefan–Boltzmann emission and an indirect effect because it influences the emission coefficient of the atmosphere. Thus, despite the fact that the epilimnetic temperature can be modelled more accurately based on the equilibrium temperature than on air temperature alone, and although it can be shown that driving variables other than air temperature, especially cloud cover, have a substantial influence on the equilibrium temperature, the only variable that we can confidently assert to be at least partly responsible for the long-term increase in the daily minimum epilimnetic temperature, and hence for the daily temperature range in the epilimnion, is the daily minimum air temperature. Nevertheless, there are strong indications that relative humidity and cloud cover should not be neglected in future modelling studies, as any long-term increase in either of these variables will act to support the effect of a long-term increase in daily minimum air temperature on the nighttime emission coefficient of the atmosphere, and hence on the nighttime emission of long-wave atmospheric radiation. This is the process that is predominantly responsible for the phenomenon of day–night asymmetry in the epilimnetic temperature.

The results of this study are not only of physical significance, but also of biological significance. The importance of water temperature as an ecological factor in lakes is undoubted, as it is a dominant regulator of nearly all physicochemical cycles and consequently of lake metabolism and productivity (Wetzel 2001). The potential biological relevance of the long-term decrease in the daily epilimnetic temperature range resulting from the increase in the daily minimum is less clear, as this is the first time to our knowledge that this phenomenon has been observed. Demonstrating experimentally the ecological implications of such a decrease is, however, likely to be a challenging task.

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Food-web responses to restoration of channel heterogeneity in boreal streams

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Abstract: We assessed the biomass and stable-isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of consumers (aquatic insects and fish (*Cottus gobio*)) and potential food sources (detritus, biofilm, seston, algae, and mosses) in channelized and restored streams in Sweden, assessing the hypotheses that restoration enhances detritus storage and detritus-based secondary production. Restored sites stored more detritus than channelized sites, with differences (+5.4% on average) prominent in margins, i.e., the channel area within 1.4 m from the banks. The biomass of other resources was similar between restored and channelized sites. Most common aquatic insects, including several putative detritivores, showed $\delta^{13}C$ values indicating reliance on aquatic (probably algal) carbon sources. The insectivorous fish *Cottus gobio*, on the contrary, appeared to be more dependent on terrestrial (detrital) carbon sources. The biomass and mean $\delta^{13}C$ values of the consumers were similar between restored and channelized sites, suggesting that restoration did not increase net secondary production or the fraction of secondary production based on detritus. We concluded that the increase in detritus storage at restored sites was either insufficient to enhance detritus-based production or the consumers were not limited by the availability of detritus.

Résumé : Nous évaluons la biomasse et la composition en isotopes stables ($\delta^{13}C$ et $\delta^{15}N$) des consommateurs (insectes aquatiques et poissons (*Cottus gobio*)) et de leurs sources potentielles de nourriture (détritus, biofilm, seston, algues et mousses) dans des cours d'eau canalisés et restaurés en Suède; nous vérifion les hypothèses selon lesquelles la restauration favorise le stockage du détritus et la production secondaire à base de détritus. Les sites restaurés accumulent plus de détritus que les sites canalisés et les différences (+5,4 % en moyenne) sont plus importantes près des bords, c'est-à-dire dans le chenal dans le premier 1,4 m de la rive. La biomasse des autres ressources est semblable dans les sites canalisés et restaurés. La plupart des insectes aquatiques, y compris plusieurs détritivores présumés, ont des valeurs de $\delta^{13}C$ qui indiquent une dépendance vis-à-vis des sources aquatiques de carbone (probablement les algues). Le poisson insectivore *Cottus gobio*, au contraire, semble être plus dépendant des sources terrestres de carbone (le détritus). La biomasse et les valeurs moyennes de $\delta^{13}C$ des consommateurs sont semblables dans les sites canalisés et restaurés, ce qui semble montrer que la restauration n'augmente pas la production secondaire nette, ni la fraction de la production secondaire à base de détritus. En conclusion, l'augmentation du stockage de détritus aux sites restaurés est insuffisante pour augmenter la production secondaire à base de détritus, ou alors les consommateurs ne sont pas limités par la disponibilité du détritus.

[Traduit par la Rédaction]

Introduction

Over the last two decades, growing public concern about environmental health has led to increasing efforts to restore degraded systems (Ormerod 2003). In streams and rivers, a widespread impact that has received much attention from restoration ecologists and practitioners is channelization, i.e., the straightening and dredging of the channel implemented for flood protection, land drainage, or transport on water (Muotka and Laasonen 2002; Pretty et al. 2003). Channelization is particularly common in boreal regions throughout the western world, where thousands of kilometres of streams and rivers have been modified through removal of flow obstructions (boulders and woody debris) and construction of embankments to facilitate the transport of timber from the watershed to the coast (Törnlund and Östlund 2002). In Scandinavia, the belief that such modifications were detrimental to fish and other biota caused the initiation of several restoration projects after the transport of timber on water ended in the1980s. In Sweden, in particular, attempts to mitigate the impacts of channelization have focused on the replacement of boulders into the channel and the removal of the stone embankments (Nilsson et al. 2005). Associated research is currently evaluating the ecological benefits of the restoration, which has provided a valuable opportunity to assess the importance of structural heterogeneity for biodiversity and ecological functions in boreal streams and rivers (Lepori et al. 2005*a*, 2005*b*).

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Forest streams are believed to be heterotrophic ecosystems relying energetically on inputs of organic detritus, represented mainly by leaves, from the surrounding terrestrial environment (Cummins et al. 1973). However, the importance of terrestrial detrital pathways in streams depends on the occurrence of structurally complex, retentive channels and is sensitive to human modifications that cause channel simplification (Webster et al. 1994; Muotka and Laasonen 2002). For these reasons, part of the research evaluating the restoration of Swedish streams has focused on the processes that control the fate of allochthonous detritus in streams, including retentiveness and decomposition (Lepori et al. 2005*a*). Work so far indicates that restoration has substantial effects on some of these controls. For example, in restored stream reaches, the retentiveness of leaves is more than 100% higher than in unrestored controls; at the same time, the mechanical breakdown of detritus is reduced at restored locations because of slower current velocities during high flows (Lepori et al. 2005*a*). We expected that these changes would improve the efficiency in the local biological use of allochthonous detritus, as a higher proportion of the total input is made available to biotic consumption instead of being lost to downstream systems (Webster et al. 1994). Given that detritivorous invertebrates in temperate streams are often resource-limited (Richardson 1991; Dobson and Hildrew 1992), we also predicted that the increased efficiency in detritus use by the biota would enhance the secondary production based on heterotrophic pathways (Lepori et al. 2005*a*).

This study assesses the consequences of the restoration of boreal streams channelized for timber transport for the structure and function of aquatic food webs. We appraised the biomass and stable isotope (^{13}C and ^{15}N) signatures of resource base (biofilm, detritus, and seston) and key consumers (aquatic insects and fish) in three pairs of restored and channelized stream reaches in the Ume River watershed, northern Sweden. Because sources of organic matter in streams tend to have different ^{13}C to ^{12}C and ^{15}N to ^{14}N ratios and because the isotopic signatures of consumers reflect those of their resource base (except for predictable changes due to fractionation at lower trophic levels), we used stable isotope analysis to assess the relative dependence of consumers on aquatic or terrestrial C and N sources (Fry 1991). Specific hypotheses were that restoration would (*i*) favor the storage of terrestrial detritus, (*ii*) enhance the total consumer biomass reliant on terrestrial detrital food chains, and (*iii*) enhance the heterotrophic character of these forest streams by benefiting detrital (heterotrophic) more than algal (autotrophic) energy pathways.

Material and methods

Study sites

Three forest streams in the Ume River watershed, northern Sweden (latitude 64°N), were chosen for this study (Table 1). In each stream, two 50 m riffle sections were identified, of which one was restored 4 to 6 years before the study and the other was still channelized. These sites were chosen to be as similar as possible in morphology except for the effects of restoration. Within each stream, sites were separated by 210–300 m of slow-flowing glides and pools, which prevent substantial transfer of organic material and organisms and strengthen the sites' reciprocal independence. Birch (*Betula pendula* and *B. pubescens*), willow (*Salix* spp.), grey alder (*Alnus incana*), and managed forests of Scots pine (*Pinus sylvestris*) surround the streams. The restoration did not affect the density and composition of the riparian trees; however, the removal of stone embankments considerably widened the channel (Table 1) and, therefore, decreased detrital inputs per unit channel area at the restored sites (Nilsson et al. 2005). Fieldwork was carried out from 18 October to 2 November 2004, shortly after leaf abscission, which in the study area is concentrated in the months of August and September (Petersen et al. 1995).

In the study streams, channelized reaches had almost all large boulders (typically 0.5–1 m in size), debris jams, and bedrock outcrops removed during the 19th and 20th centuries to facilitate the transport of timber. The boulders removed were used to build embankments on each side of the stream, which narrowed and deepened the channel and cut off backwaters where the floating logs could have become stranded. The restoration activities consisted mainly of using bulldozers to remove the stone walls and replace approximately 80%–90% of the boulders into the channel. In addition to the widening of the wetted channel, obvious effects of the restoration include an increase in hydraulic complexity and a decrease in the reach-averaged current velocity (Table 1). Further information on the restoration schemes is given by Lepori et al. (2005*a*) and Nilsson et al. (2005).

Studies evaluating restoration projects should compare restored with unrestored sites to assess if the restoration is producing any changes and restored with reference sites to assess if the changes are towards the desired direction (Barmuta 2002). The present study did not include reference sites because its primary focus was not to evaluate the success of the restoration schemes, but to assess generally the importance of structural heterogeneity to the pathways of energy in the study streams. To this end, only a comparison between heterogeneous and homogeneous stream reaches is relevant. Thus, channelized stream reaches were chosen to represent homogeneous conditions. Heterogeneous conditions were represented by restored rather than reference (i.e., near-pristine) reaches to allow designing the study as a paired comparison, with treatments compared within the same streams, to minimize the confounding effect of variation unrelated to structural heterogeneity (e.g., in temperature, riparian cover, stream size, etc.). In the study area, reference reaches are found mostly in small streams unsuitable for timber transport and rarely co-occur with channelized reaches (Nilsson et al. 2005).

Standing stocks of potential food sources and consumers

Storage of benthic detritus was quantified as the percentage of streambed covered by leaves and leaf fragments excluding needles, which are probably unimportant as food to detritivorous invertebrates compared with broadleaves. We used a stratified design to sample channel "margins" (channel area within 1.40 m from each bank) separately from the "midchannel" area (area between the margins), because preliminary observations suggested that margins contribute disproportionately to detritus storage in the study streams. Fourteen random spots were sampled within each stratum at

Table 1. Characteristics of three pairs of channelized (Ch.) and restored (Re.) stream sites in northern Sweden studied for food-web structure and carbon and nitrogen pathways in autumn 2003.

Stream	Maltan		Ramsan		Tannbäcken	
	Ch.	Re.	Ch.	Re.	Ch.	Re.
Order	3	3	4	4	3	3
Watershed (km^2)	120	120	356	356	204	204
Years since restoration	—	6	—	6	—	4
Width (m)[a]	7.9	13.4	8.8	14.6	8.0	10.7
Depth (m)[a]	0.20	0.16	0.23	0.23	0.28	0.16
Current velocity ($m \cdot s^{-1}$)[a]	0.24	0.13	0.45	0.29	—	0.11
Flow ($m^3 \cdot s^{-1}$)[a]	0.4	0.3	0.9	1.0	0.2	0.2
pH[a]	6.9	6.9	6.8	6.8	6.9	6.9
Conductivity ($\mu S \cdot cm^{-2}$)[a]	23	23	24	24	30	30
Aquatic mosses (% coverage)	64	35	82	82	—	14.2
Shading by canopy (%)[b]	36.7	36.8	35.8	37.2	—	32.1

Note: Data from Lepori et al. (2005*a*) and D. Gaul (unpublished data).

[a] During summer base flows.

[b] Average slope between the centre of the stream and the top of the canopy measured in upstream, downstream, right, and left direction. The data in the table are the mean of 10 measurements taken at equidistant points at each study site.

each site. At each spot, detritus cover was estimated by laying a gridded frame (0.7 m × 0.7 m, divided into 49 squares) onto the streambed and recording the presence or absence of leaf litter (>1 cm) in each square with the help of a viewing box and a torch. The cover of detritus within each frame was expressed as the percentage of squares containing detritus out of the total number of squares (49), excluding squares with >50% of outcropping (dry) substratum. The width of the margins (1.40 m) was chosen because it matched a natural discontinuity between depositional habitats next to the banks and faster-flowing areas in the midchannel.

Our approach to quantify benthic detritus was validated in a pilot test, which showed that the percentage cover of detritus was strongly associated with its standing stock (grams of ash-free dry mass (AFDM) per square metre) at both the restored ($n = 5$, $r = 0.99$, $p = 0.002$) and the channelized ($n = 4$, $r = 0.92$, $p = 0.079$) sites of the stream Tannbäcken. The regression

$$\text{detritus standing stock (g AFDM}\cdot\text{m}^{-2}) = 1.39 \times \text{detritus area coverage (\%)} - 12.3$$

fits our results well ($R^2 = 0.94$) and might be used to convert detritus area coverage into standing stocks for comparisons with other studies. For the pilot test, after the determination of percentage cover, detritus within the frame at each sampling spot was collected in a kicknet (mesh size 250 μm) and brought to the laboratory for AFDM determination through 1 h combustion at 500 °C.

To assess the effect of restoration on algal resources and compare it with the effect on detritus, biofilm standing stocks at channelized and restored sites were quantified as chlorophyll *a* and AFDM density ($mg \cdot m^{-2}$). Biofilm was collected from the upper surface of 10 randomly selected rocks per site using a sampler consisting of a rotating nylon brush (width 6 cm) and a vacuum pump that draws the scrubbed biofilm sludge into plastic jars (Persson et al. 2006). Biofilm samples, immediately protected from light, were deep frozen within 4–5 h of collection. In the laboratory, the thawed biofilm sludge was collected on pre-ashed Whatman GF/F filters. The filters were subsequently cut into two identical parts, one of which was used for chlorophyll *a* analysis and the other for AFDM analysis. Chlorophyll *a* was determined by fluorometry (Luminescence Spectrometer LS45; PerkinElmer, Life and Analytical Sciences, Monza (Milan), Italy) following extraction in ethanol for 24 h at 2 °C.

Benthic insects and fish, almost exclusively bullhead, *Cottus gobio* L., were sampled using an electroshocker and a kicknet (frame 0.7 m × 0.4 m; mesh size 250 μm) to collect the drifting animals (Lepori et al. 2005*b*). Standardized samples were collected from 20 random patches (1 m long) per site. Bullheads from all samples were measured to the nearest millimetre before they were returned alive to the water. Insects from a random subset of six samples were fixed in ethanol and brought to the laboratory, where they were sorted using a two-phase procedure (Vinson and Hawkins 1996). To this end, samples were divided into small (250 μm to 1.3 mm) and coarse (>1.3 mm) fractions using nested sieves. The coarse fractions were fully sorted, whereas the small fractions were subsampled using a Folsom sample splitter (Van Guelpen et al. 1982) until aliquots of estimated 100–200 individuals were obtained. Insects were identified to species or genus (except for Diptera, which were identified to family) and attributed to functional feeding categories according to Merritt and Cummins (1996) and Tachet et al. (2002). The head-capsule width of 5–10 individuals per insect species was measured (±0.1 mm) to estimate dry biomass from published regression models (Meyer 1989). Bullhead biomass (W, g) was estimated from length (L, mm) using a regression equation ($\log W = -2.10 + 3.17 \log L$; $r^2 = 0.98$) derived from 60 individuals, 10 per site, collected during our study. Before regression analysis, we ensured that the slope of the relationship between $\log W$ and $\log L$ was consistent across all study sites (analysis of covariance, df = 5, $F = 0.51$, $p = 0.764$).

Stable isotope analysis (SIA)

Terrestrial leaves, biofilm, benthic organic detritus, seston, filamentous algae, and aquatic mosses were sampled to represent the potential basal resources in the study streams.

Composite samples of leaves were collected from all riparian tree species at each study site just before abscission. Biofilm was scrubbed from the upper surface of 4–5 stones using a brass-wire brush. Benthic detritus was collected using a hand-net (mesh size 25 µm); organic matter was later elutriated from mineral detritus (sand and clay) and wet-sieved to separate coarse particulate organic matter (CPOM, >1 mm) from fine particulate organic matter (FPOM, 25 µm – 1 mm). Seston was obtained from 20 L grab samples of stream water. Filamentous algae and aquatic mosses were hand-removed from submerged rocks. Before laboratory processing, all samples were deep frozen except for stream water, which was stored in the dark at 8 °C. Next, all samples except seston were dried (72 h at 50 °C) and ground using either a coffee grinder or a mortar and pestle. Seston was collected on Whatman GF/F filters by filtering 1.7–3.5 L of stream water per site and dried.

Aquatic insects and bullheads, representing the most important consumers in the study streams, were collected using electroshocking. Insects for SIA were among those not used for density and biomass assessment (i.e., from 14 out of the 20 sampling spots per site). They were pooled in a plastic container filled with stream water and stored alive overnight to allow gut clearance before being deep-frozen. Ten bullheads per site, of which five were juveniles (0+ years) and the other five were 1 to 3 years old, were immediately deep-frozen in the laboratory. The insect species considered for SIA were a subset chosen to comprise >90% of the total insect biomass at each study site based on the six benthic samples analyzed for biomass (see Results). Whole-body insects and bullhead muscle tissue cut from behind the dorsal fin were dried at 50 °C for 72 h and ground using a mortar and pestle.

Before the stable isotope analyses, aliquots (2.3–6.6 mg) of each sample were transferred into 5 × 10 or 5 × 12 mm tin capsules. The filters upon which seston was collected were cut into 5 mm discs using a hole-puncher, and 13 discs per site were stacked into 5 × 12 mm tin capsules. Blank filters were likewise processed to allow the determination of the stable-isotope signatures of seston alone using the mixed model:

$$R_{\text{seston}} = (R_{\text{whole sample}} - R_{\text{blank}}\ p_{\text{f}})/(1 - p_{\text{f}})$$

where $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$, "blank" is the sample containing only blank filters, "whole sample" is the sample containing both filters and seston, and $p_{\text{f}} = \text{mass}_{\text{blank}}/\text{mass}_{\text{whole sample}}$.

Analysis of ^{13}C and ^{15}N stable isotopes was carried out on an isotope ratio mass spectrometer (ANCA-SL; Europa Scientific, Crewe, UK) at the Swedish University of Agricultural Sciences in Umeå, Sweden.

Data analysis

The trophic status of the biofilm was characterized using the autotrophic index (AI; Steinman and Lamberti 1996), which expresses the proportion of the organic biofilm that is photosynthetic (autotrophic):

$$\text{AI} = \text{AFDM}/\text{chlorophyll } a$$

Note that AI increases with increasing degree of heterotrophy. Values of AI between 50 and 200 are considered the norm in unpolluted streams.

Stable isotope composition was expressed as δ values, i.e., the difference in parts per thousand (‰) between the isotopic ratio of the sample and that of a standard (PeeDee Belemnite formation for C and atmospheric nitrogen for N):

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

To assess any shifts in the use of terrestrial versus aquatic resources by aquatic insects, the average insect δ^{13}C, weighted by species biomass, was compared between paired unrestored and restored sites. Fractionation rates (see Introduction) are typically 0‰–1‰ δ^{13}C and 3‰ δ^{15}N with each trophic level (Minagawa and Wada 1984; Fry 1991).

In this study, replication at the treatment level was limited ($n = 3$) because of the high cost and intensive labor involved in the analysis of stable isotopes. Given the low statistical power associated with such a level of replication, we did not consider it useful to evaluate the significance of our results using formal statistical tests. Instead, we had to base inference on the consistency and magnitude of the responses observed, as well as on careful scrutiny of the results in the light of ecological theory and empirical knowledge of the study area. Our conclusions assume that the differences in the response variables between our treatments that we considered ecologically meaningful did not arise by chance or through systematic differences in environmental characteristics unrelated to restoration. We believe that the paired design of the study and the cautious interpretation of the results substantially contributed towards satisfying these assumptions.

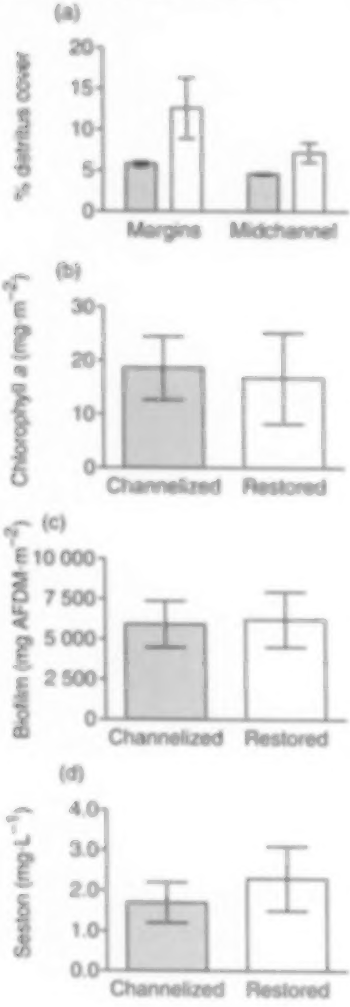
Results

Standing stocks of potential food sources and consumers

In the midchannel area, detritus cover was similar at restored and channelized sites (Fig. 1*a*). Along the margins, by contrast, detritus cover was higher at restored sites (range of the difference between paired restored and channelized sites –1.2% to +12.3% cover, average +5.4%; Fig. 1*a*). Across all sites, margins stored more detritus (+2.2% to +13.7% cover, average +4.7%) and showed higher variation in detritus cover (standard error (SE) 2.0 versus 0.6) than midchannel areas (Fig. 1*a*). Biofilm standing stocks (5.1–33.3 mg chlorophyll $a\cdot\mathrm{m}^{-2}$ and 3086–9590 mg $\mathrm{AFDM}\cdot\mathrm{m}^{-2}$) were similar at channelized and restored sites (Figs. 1*b* and 1*c*), whereas the autotrophic index (256–1149) was consistently higher at restored sites (+12 to +561, average +357), indicating higher proportions of non-algal organic material. The concentration of seston (1.1–3.8 mg $\mathrm{AFDM}\cdot\mathrm{L}^{-1}$) was comparable between restored and channelized sites (Fig. 1*d*), except in the stream Ramsan where it was slightly higher at the restored site (+1.1 $\mathrm{mg}\cdot\mathrm{L}^{-1}$).

With the exception of one individual grayling (*Thymallus thymallus*), bullhead was the only fish found at the study sites. Bullhead biomass values ranged between 0.6 and 3.9 g wet $\text{weight}\cdot\text{sample}^{-1}$ and were similar at restored and channelized sites (Fig. 2*a*). By contrast, bullhead numbers ($\text{no.}\cdot\text{sample}^{-1}$) were consistently higher at the restored sites (+15% to

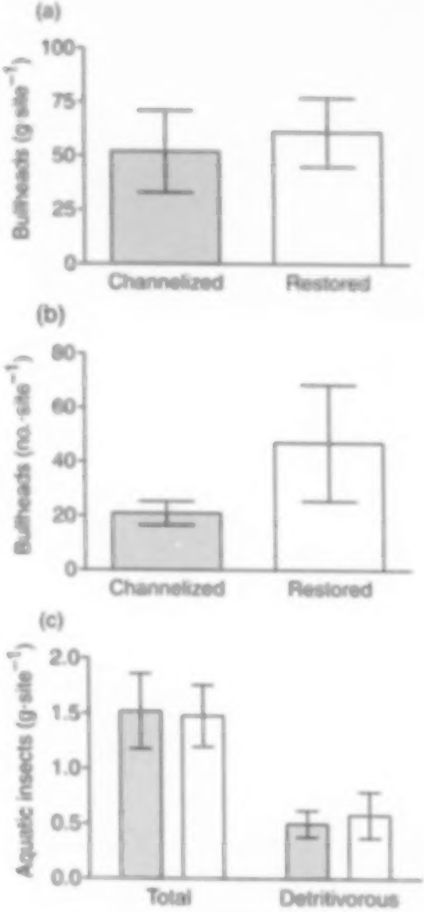
Fig. 1. Standing stocks (average ± standard error) of resource base in channelized and restored streams in northern Sweden ($n = 3$): (*a*) detritus (quantified separately in marginal and midchannel habitats; shaded bars, channelized sites; open bars, restored sites); (*b*) benthic algae (quantified as chlorophyll *a* in the biofilm); (*c*) whole biofilm; and (*d*) seston.



+214%, average +101%) relative to channelized conditions, indicating that the restored sites had more but smaller fish (Fig. 2*b*).

Total biomass of aquatic insects (144–331 mg DM·sample^{-1}) showed small and inconsistent differences between restored and channelized sites (–13% to +8%, average 0%; Fig. 2*c*). The functional organization of insect assemblages varied between sites with no clear pattern. Shredders (11%–66% of the total insect biomass across the sites) and all putative detritivores (i.e., shredders and deposit feeders; 12%–67% of total insect biomass) had slightly higher biomass values at restored than at channelized sites (average +18%) because of a substantial difference between sites in one stream (Ramsan) driven by patterns in *Taeniopteryx nebulosa* distribution (Fig. 2*c*). Grazers (mostly the mayflies *Baetis rhodani* Pict. and *Heptagenia sulphurea* Müller), representing 7%–49% of total insect biomass, had similar biomass between restored and channelized sites, except in the stream Tannbäcken where *B. rhodani* was exceptionally abundant at the restored site. Predators (*Isoperla grammatica* Poda and *Diura* spp.) were scarce overall (3.1%–9.7% of total insect biomass), whereas filter-feeders (mainly *Hydropsyche pellucidula* Curtis and *H. siltalai* Döhler) were abundant (3.4%–74% of total insect biomass), particularly at channelized sites (+17% on average) relative to restored sites.

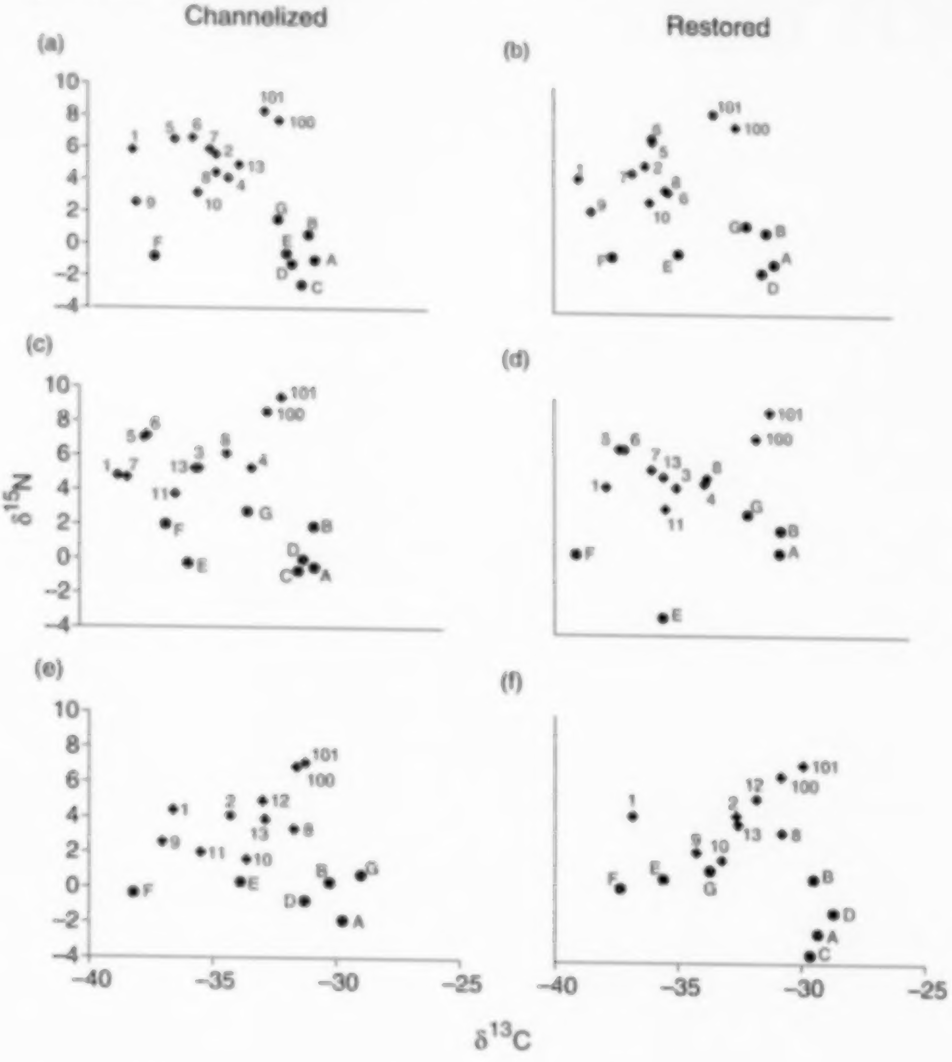
Fig. 2. (*a*) Biomass and (*b*) abundance (average ± standard error) of bullhead and (*c*) biomass of aquatic insects (total and detritivores only) from channelized and restored streams in northern Sweden ($n = 3$).



Stable isotope analysis

The $\delta^{13}C$ and $\delta^{15}N$ values of the resource base and key consumers at the study sites are shown (Fig. 3). Mosses and filamentous algae, representing end points of aquatic carbon (assuming that their $\delta^{13}C$ was representative of 100% autochthonous organic carbon), were considerably depleted in ^{13}C compared with terrestrial leaves, which represent the end point of terrestrial carbon. CPOM and FPOM had very

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of resource base and consumers from channelized and restored sites in three Swedish streams: (*a*) Ramsan channelized; (*b*) Ramsan restored; (*c*) Tannbäcken channelized; (*d*) Tannbäcken restored; (*e*) Maltan channelized; (*f*) Maltan restored. Circles represent potential resource base: A, coarse particulate organic matter (CPOM); B, fine particulate organic matter (FPOM); C, needles; D, broadleaves; E, filamentous algae; F, mosses; and G, biofilm. Diamonds represent consumers (putative functional feeding groups are shown in parenthesis): 1, *Baetis rhodani* (grazer); 2, *Heptagenia sulphurea* (grazer); 3, *Heptagenia dalecarlica* (grazer); 4, *Lepotophlebia marginata* (deposit feeder); 5, *Hydropsyche pellucidula* (filter feeder); 6, *Hydropsyche siltalai* (filter feeder); 7, *Isoperla grammatica* (predator); 8, *Leuctra hippopus* (shredder); 9, *Protonemura meyeri* (shredder); 10, *Taeniopteryx nebulosa* (shredder); 11, *Amphinemura* spp. (shredder); 12, *Diura nanseni* (predator); 13, *Simuliidae* (filter feeder); 100, 0+ age class bullheads (*Cottus gobio*); 101, ≥1 age class bullheads.



similar $\delta^{13}C$ values to those of riparian leaves. In most cases, the $\delta^{13}C$ values of the biofilm were close to those of terrestrial detritus, consistent with the high AI values of the biofilm samples (see above) and observations that algae (mainly diatoms) were scarce in the biofilm's amorphous matrix (D. Gaul, unpublished data). The stable isotope concentrations of seston were highly variable ($\delta^{15}N$, 5.4 to 9.7; $\delta^{13}C$, −38.4 to −23.3) and inconsistent with those of seston feeders (e.g., Simuliidae, see Fig. 3), suggesting that analytical errors might have occurred. They were not considered further.

Twelve species of aquatic insects, from seven to 10 per site, were considered for SIA (Fig. 3). These subsets represented 92%–95% of the total insect biomass found at each site. Overall, the $\delta^{13}C$ values of aquatic insects reflected the values of mosses and algae, implying a prevailing contribution of aquatic carbon (probably derived from algae, as consumption of moss is rare among invertebrates) to insect production. However, some species, particularly *Leuctra hippopus* Kempny (shredder) and *Leptophlebia marginata* L. (deposit feeder), showed enrichments in ^{13}C indicating a partial reliance on terrestrial detritus.

Bullheads in both the 0+ and the ≥1 age classes were enriched in ^{13}C by approximately 3.5‰ compared with aquatic insects. Even accounting for some fractionation as C isotopes are transferred up the food web, the δ^{13}C values of bullheads imply reliance on terrestrial rather than aquatic carbon sources. Consistent with their top trophic position in the food webs examined, bullheads were the most ^{15}N-enriched consumers; moreover, fish in the ≥1 age class were slightly (<1‰) but consistently ^{15}N-enriched relative to fish in the 0+ age class. Differences in bullhead δ^{13}C values between restored and paired channelized sites were small (–0.74‰ to +1.31‰) and inconsistent in direction.

Discussion

Our first hypothesis, that restored sites would store more terrestrial detritus than channelized sites in view of the higher retentiveness (Lepori et al. 2005*a*), is partly supported by the results of the study, even though differences were apparent only along the margins, where restoration recreated depositional eddies and lateral niches that were rare at channelized sites. Surprisingly, however, the difference in detritus storage between channelized and restored sites was much smaller than the difference in short-term (3 h) retentiveness (+135% to +328%) recorded at the same sites in a previous study (Lepori et al. 2005*a*). Part of the discrepancy between storage and retentiveness probably is due to the widening of the channel caused by the removal of the embankments built as part of the channelization of the streams: this restoration activity counteracts the effect of retentiveness by decreasing the inputs of detritus per unit of channel area. In addition, it seems likely that detritus storage and retentiveness were different at the study sites because they are controlled by distinct mechanisms. In streams, leaf retentiveness has often been attributed to trapping by flow obstructions in lotic habitats rather than deposition in dead channel zones (Speaker et al. 1984; Webster et al. 1994). In a previous study, we supported this view, showing that retentiveness at our study sites was strongly associated with the density of boulders and woody debris (Lepori et al. 2005*a*). However, the present study suggests that the retention of leaves by flow obstructions is transient, and long-term storage requires the deposition in the tranquil pockets along the margins. These findings corroborate and extend to small watercourses ideas anticipated by the Riverine Productivity Model (Thorp and Delong 1994), which proposed that in large-river ecosystems nearshore habitats play a key role in the storage and processing of terrestrially derived CPOM. Therefore, besides their known roles as flow refugia for invertebrates (Negishi et al. 2002) and nurseries for fish (Sempeski and Gaudin 1995), heterogeneous channel margins also create conditions conducive to the transfer of energy from terrestrial to aquatic systems; given such multiplicity of ecological roles, margins clearly deserve a special consideration in projects aiming at conserving or restoring running-water systems.

Our second hypothesis, that the biomass of consumers relying on detrital food chains would be higher at restored than channelized sites, was not supported by the study; the total consumer biomass and the relative contribution of terrestrial versus aquatic carbon sources to consumer biomass were similar between treatments. Our hypothesis stemmed from evidence that detritus availability in streams limits the production of detritivorous insects (Richardson 1991; Dobson and Hildrew 1992) and has ramifications for other functional groups (Wallace et al. 1997). Several reasons can explain the apparent lack of food-web response to restoration. First, the effects of restoration on detritus storage might have been insufficient to affect detritivore production or prompt higher detritus consumption in generalist consumers. Second, detritivores at our study sites might be controlled by factors other than leaf detritus availability, either because physicochemical factors are most limiting (Hoffsten 2003) or because alternative resources (e.g., decomposing mosses and algae) are abundant. Given that in northern boreal streams inputs of leaf litter are naturally scarce (Haapala and Muotka 1998), plasticity in feeding habits and reliance on alternative food sources might be expected in detritivores. Third, restoration might have increased heterotrophic production, with effects confined to newly created depositional niches along the channel margins. In this case, either a more intensive or a more targeted (e.g., Haapala et al. 2003) biotic sampling would have been necessary to detect the food-web effects of restoration. Finally, the consumption of detritus might have increased detritus-based production and changed the consumers' isotopic signature at the restored sites, but these effects were blurred by a redistribution of detritivores over larger stream sections. In the study streams, the scale of the restoration is typically a few hundred metres of channel length and is commensurable with the range of movement of aquatic insects (up to tens of metres per week; Erman 1986). Therefore, emigration to neighbouring reaches could have diluted the extra production of detritivore insects at the restored sites. However, in streams where leaf detritus is a limiting resource base, a local increase in detritus availability is more likely to attract detritivores from surrounding areas than to cause net emigration (Richardson 1991). Therefore, any redistribution of organisms within the streams should have amplified, not diluted, the differences in detritivore biomass between restored and channelized sites.

Given that the study streams, even though they flow through dense boreal forests, are relatively wide and not completely shaded, it was expected that autotrophic pathways would substantially contribute to insect production. A striking result of this study, however, was how unimportant heterotrophic pathways appear to be. Although carbon from terrestrial origin was apparently abundant in the study streams and putative detritivores were well represented in the benthic assemblages (42% of the total insect biomass on average), insect production was largely driven by aquatic carbon. Such apparent bias towards algal consumption is inconsistent with the river continuum concept (RCC; Vannote et al. 1980), one of the most influential frameworks of stream ecosystems, which proposes that lotic invertebrate communities maximise the use of energy available by tuning their functional organisation (relative abundance of functional feeding groups) to match the abundance of the resources present. In contrast, our results support growing empirical evidence indicating that the use of autochthonous (algae) versus allochthonous (leaves) food resources by stream biota is often decoupled from their relative availability and that the importance of terrestrial carbon has probably been overestimated by the RCC and other related conceptual models of stream ecosystems (e.g., Finlay 2001; Bunn et al. 2003). Also, the mismatch between the functional feeding group classification and the actual trophic role of some aquatic insects in this study, which is consistent with several other studies, undermines the often-held assumption that functional feeding group composition reflects the heterotrophic or autotrophic character of a stream (Mihuc (1997) and references therein). In general, our results imply that aquatic insects, including putative shredders, preferentially feed on algal resources even when detritus is abundant, probably because algae have better nutritional qualities (e.g., a C to N ratio of ~10 compared with ~15 for terrestrial leaves; Giller and Malmqvist 1998). Here too, our results support the riverine productivity model (Thorp and Delong 1994), which emphasizes that the importance of different sources of carbon as food for lotic macroinvertebrates depends at least as much on their accessibility and ease of assimilation as on their total abundance.

The dependence of bullheads on terrestrial carbon is perplexing because it is inconsistent with the aquatic-carbon signature of the insects in the study streams, which include many potential prey, and with previous food-web research, which showed that the importance of heterotrophic versus autotrophic carbon sources tends to decrease towards higher trophic levels (Peterson et al. 1993; Thorp et al. 1998). Possible explanations are that either bullheads selectively prey on the invertebrates most dependent on terrestrial detritus or that terrestrial carbon is more prominent in invertebrate tissues in spring and summer, when bullhead growth is most intense. More dietary information, ideally addressing seasonal changes, would be needed to clarify this apparent inconsistency in our results.

Many restoration schemes in streams and rivers rely so strongly on the assumption that the enhancement of structural complexity is beneficial to biodiversity and ecosystem functioning that follow-up work is rarely implemented (Palmer et al. 1997; Bash and Ryan 2002). Our study emphasizes the dual value of evaluative studies. On one hand, we showed that ecological effects of habitat restoration in streams are difficult to predict, especially in view of apparent limitations in current frameworks of stream ecology. On the other hand, the improved ecological understanding resultant from the study might offer better guidance to future management endeavors.

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The effect of suspended sediment on fertilization success in sockeye (*Oncorhynchus nerka*) and coho (*Oncorhynchus kisutch*) salmon

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Abstract: Suspended sediment is a naturally occurring part of aquatic ecosystems, and unnatural elevation of suspended sediment in streams above background concentrations is known to adversely affect Pacific salmon (*Oncorhynchus* spp.) at different life stages. Conspicuously lacking in the literature is knowledge of the effect of suspended sediment on egg fertilization success during spawning. Sockeye (*Oncorhynchus nerka*) and coho (*Oncorhynchus kisutch*) salmon gametes were used to investigate the impact of different concentrations of suspended sediment particles on the ability of sperm to successfully fertilize eggs. The fertilization process was simulated using a controlled-flow water flume with concentrations of suspended particles ranging from 800 to 47 000 $mg \cdot L^{-1}$. Egg fertilization success was assessed at eyed stage after incubating eggs in the streambed in the field or in artificial laboratory egg incubation (Heath) trays. Regression model analysis showed that suspended sediment concentrations reduced the percent of fertilized eggs and that reduction in successful fertilization below 80% could occur when suspended sediment levels are in excess of 9000 $mg \cdot L^{-1}$. The relationship derived herein serves as a preliminary guideline for determining the effect size of suspended sediment concentration on egg fertilization success during spawning.

Résumé : Les sédiments en suspension sont une composante naturelle des écosystèmes aquatiques, mais toute élévation artificielle des concentrations de sédiments en suspension au-delà des valeurs de base affecte négativement les saumons du Pacifique (*Oncorhynchus* spp.) aux différentes étapes de leur cycle. Il existe une absence flagrante d'information dans la littérature sur l'effet des sédiments en suspension sur le succès de la fécondation des oeufs durant la fraye. Nous utilisons des gamètes de saumons rouges (*Oncorhynchus nerka*) et coho (*Oncorhynchus kisutch*) pour déterminer l'impact de différentes concentrations de sédiments en suspension sur la capacité des spermatozoïdes à féconder les oeufs avec succès. Nous avons simulé le processus de fécondation à l'aide d'un canal à débit d'eau contrôlé avec des concentrations de particules en suspension variant de 800 à 47 000 $mg \cdot L^{-1}$. Nous avons évalué le succès de la fécondation au stade de l'oeuf nucléé après une incubation des oeufs dans le fond du ruisseau en nature ou dans des plateaux artificiels d'incubation (de Heath) en laboratoire. Une analyse par modèle de régression montre que les concentrations de sédiments en suspension réduisent le pourcentage d'oeufs fertilisés et qu'une réduction du succès de la fécondation à moins de 80 % peut se produire à des concentrations de sédiments en suspension supérieures à 9000 $mg \cdot L^{-1}$. La relation que nous avons trouvée peut servir de repère préliminaire pour déterminer l'importance de l'effet de la concentration de sédiments en suspension sur le succès de la fécondation des oeufs durant la fraye.

[Traduit par la Rédaction]

Introduction

This research focuses on the potential effect of suspended sediments on Pacific salmon (*Oncorhynchus* spp.) egg fertilization success in streams. Many studies have examined the effects of suspended sediment on adult and juvenile salmon (see review by Newcombe and Jensen 1996) and on physical alteration of fish habitat (Anderson et al. 1996). Chapman (1988) reviewed the studies of sediment effects on salmonid reproduction and detailed the impacts on embryos during incubation and subsequent alevin development, but to date, no research has investigated the potential problem of detrimental effects on egg fertilization success during spawning.

This is perhaps surprising given that salmonids spawning in freshwater streams are so potentially vulnerable to elevated suspended sediment particle concentrations resulting from

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natural or anthropogenic sediment inputs. Salmonids are oviparous and their gametes combine outside the body cavity, making them susceptible to external environmental influences such as suspended sediments that might impede egg–sperm contact. The spawning process leading to egg fertilization begins when salmon dig a depression (a redd) in the streambed, producing a pocket of low or back-eddying water flow and creating a medium where the opportunities for egg–sperm contact are maximized. Suspended sediment particles could affect fertilization success by interfering with sperm mobility and sperm–micropyle encounter rates or by causing micropyle blockage preventing sperm entry into the egg.

Suspended sediments occur naturally in streams and are an integral component of aquatic ecosystems (Birtwell 1999). Their concentrations vary throughout the season in response to natural hydrological changes and natural channel erosion events generally caused by hydrologic fluctuations. Certain concentrations of suspended sediment directly kill fish (Birtwell 1999). For adult salmonids, Newcombe and Jensen's (1996) severity-of-ill-effect model indicates that mortality can occur after a week of exposure in the 1000 $mg \cdot L^{-1}$ suspended sediment range or after a matter of hours when concentrations reach greater than 10 000 $mg \cdot L^{-1}$. Most streams have very low concentrations of suspended sediments during spawning (e.g., <20 $mg \cdot L^{-1}$; Cheong et al. 1995), but some can have periods of much higher suspended sediment (e.g., >5000 $mg \cdot L^{-1}$ in the Chilliwack River (D.W. Martens, Fisheries and Oceans Canada, Cultus Lake, BC V2R 5B6, personal communication); >11 000 $mg \cdot L^{-1}$ in the Red Deer and Peace rivers (Anonymous 1980 in Lake and Hinch 1999)).

Land and water use practices that increase concentrations of suspended sediment above the natural range pose a threat to the freshwater spawning, incubation, and rearing habitats of salmonids that are particularly sensitive to excess sediment. Anthropogenic influences such as mining (Birtwell 1999), road building, and forest harvesting (Beschta 1978) are all risk factors for sudden, elevated sediment inputs into lotic systems. Naturally occurring channel erosion, upslope and streambank failures, and catastrophic events such as volcanic eruptions (Martin et al. 1984) can also significantly increase suspended sediment levels over background values. Even redd digging by salmon can "winnow" sediment from the streambed, causing increased suspended sediment concentrations during spawning (Cheong et al. 1995).

The concentration of suspended sediment that adversely impacts egg fertilization is important from a fish and fish habitat management perspective. To complement existing data on sediment–salmon interactions and to improve resource management decision-making about harmful levels of suspended sediment, the relationship between concentration of suspended sediment and egg fertilization success needs to be defined. No such information on suspended sediment and egg fertilization currently exists. In this paper, the hypothesis is that elevated concentrations of suspended sediment particles would reduce egg fertilization success in salmonids. To test this hypothesis, an investigation of egg fertilization – suspended sediment interactions was conducted with Early Stuart sockeye salmon (*Oncorhynchus nerka*) in the field and Chilliwack River coho salmon (*Oncorhynchus kisutch*) in the laboratory.

Materials and methods

Study sites

The field study took place at Kynoch Creek, a tributary to Middle River immediately south of Takla Lake, part of the upper Fraser River drainage system in British Columbia. Kynoch Creek is a major spawning stream for the Early Stuart sockeye salmon stock (Macdonald et al. 1992) and is one of four study watersheds where research is currently being conducted on forest harvesting impacts (Macdonald 1994). Kynoch Creek experiences natural fluctuations in suspended sediment concentrations: in spring freshet, they can reach 120 $mg \cdot L^{-1}$, but values rarely exceed 20 $mg \cdot L^{-1}$, and during summer low water flow, concentrations are typically less than 5 $mg \cdot L^{-1}$ (Cheong et al. 1995).

The laboratory study was conducted at the Fisheries and Oceans Canada Laboratory, Cultus Lake, British Columbia, using coho salmon collected from the Chilliwack River Hatchery. The Chilliwack River is a direct tributary into the lower Fraser River and is subject to large natural fluctuations in suspended sediment. During high water flows, suspended sediment concentrations can be greater than 5000 $mg \cdot L^{-1}$ (D.W. Martens, Fisheries and Oceans Canada, Cultus Lake, BC V2R 5B6, personal communication). However, the ambient concentration of suspended sediment in the water supplied from Cultus Lake to the laboratory, and used in this experiment, was less than 3 $mg \cdot L^{-1}$.

Gamete collection

Gametes were collected from sockeye or coho salmon that were ready to spawn as per Springate et al. (1984): when milt or eggs were easily extruded upon gentle abdominal pressure, sperm and eggs were then stripped by anterior to posterior abdominal massage. All gametes were stored in clean plastic containers and kept in an insulated cooler (approximately 4 °C). Fertilization trials began within an hour after gamete collection. Care was taken to prevent contamination of the gametes with water during collection, storage, and handling, which can cause premature sperm and egg activation that decreases gamete viability. Pooled gametes were a mixture of eggs or milt from more than one adult; paired gametes were eggs or milt from a single male and female matched for the entire experiment (see below).

Pooled gamete experiments

Sockeye salmon (1999)

On 15 and 16 August 1999, 9 male and 12 female sockeye salmon were collected from Kynoch Creek. Three milt and four egg pools were generated with gametes using three different fish of each sex. Ten replicate trials were conducted with three suspended sediment treatments and a control (Table 1). Trials were carried out in a randomized complete block design, randomly conducting all treatments within each block.

Sockeye salmon (2000)

On 7 August 2000, five male and six female sockeye salmon were collected from Kynoch Creek, and gametes combined into one pool of milt and one pool of eggs. Ten replicate trials were conducted with one suspended sediment

Table 1. Mean measured suspended sediment concentrations (mg·L^{-1}) ± standard error (SE) in a water flume to which sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon gametes were exposed during fertilization and resultant fertilization success.

					Fertilization	
Species	Experiment	No. pools or pairs	*n*	Suspended sediment, mg·L^{-1} (±SE)	Unadjusted, % (±SE)	Adjusted, percentage of control
Sockeye	Pooled 1999	3–4	10	44 (10)	35.3 (4.8)	100
			10	798 (23)	34.7 (4.7)	99.2
			10	1 828 (47)	31.5 (4.2)	99.9
			10	6 621 (120)	26.2 (5.4)	78.4
Sockeye	Pooled 2000	1	10	128 (26)	51.0 (4.7)	100
			10	46 943 (1412)	7.5 (1.1)[a]	14.7
Sockeye	Paired 2000	5	10	71 (14)	41.9 (5.5)	100
			10	7 691 (278)	30.1 (6.2)	72.7
			10	38 231 (1987)	17.3 (4.1)[a]	38.7
Coho	Pooled 1999	1	4	22 (7)	61.4 (11.3)	100
			2	4 095 (289)	41.0 (4.3)	66.8
			3	28 835 (2263)	31.2 (6.3)[a]	50.8

Note: Fertilization success is reported as unadjusted (%) and adjusted as a percentage of control mean for that sockeye or coho gamete pool (pooled gametes, 1999 or 2000) or sockeye gamete pair (paired gametes, 2000).

[a] Indicates statistically significant difference from that experiment's control ($P < 0.05$).

treatment and a control (Table 1). The order of trials for these two treatments was randomized.

Coho salmon (1999)

On 30 November 1999, nine male and nine female coho salmon were captured at the Chilliwack River Hatchery. Their gametes were collected in separate containers and transported a short distance to the Cultus Lake Laboratory. Two milt and egg pools were generated with gametes using three different fish of each sex. Nine replicate trials were attempted with two suspended sediment treatments and a control (Table 1). Trials were conducted according to a randomized complete block design, randomly conducting all three treatments within each block.

Paired gamete experiment

Sockeye salmon (2000)

To test and control for differences in gamete quality among individuals, milt and eggs from eight male and eight female sockeye salmon were collected on 4 and 5 August 2000 from Kynoch Creek and were randomly combined into fertilization pairs. These pairs of gametes were matched for the entire experiment. Only males yielding greater than 10 mL milt were used. Two replicates with two treatments and a control (Table 1) were performed with each pair, providing each treatment with 16 trials.

Water flume

A 3 L water flume was designed to provide control of suspended sediment concentrations and repeatability of the experimental conditions for sequential replications of gamete exposure. The 1 m long flume was constructed from one-half of a 10 cm diameter ABS (acrylonitrile–butadiene–styrene) pipe cut lengthwise to create a round-bottom trough, the ends of which were capped with either a water inflow or an outflow port. A pump drew water from one end of the trough and released it into the other end through 2 cm diameter flexible plastic tubing. A valve placed at the outlet of the pump could be adjusted to control water flow. A plastic straw bundle at the inflow end of the flume created a more laminar flow, reducing turbulence and providing an even distribution of suspended sediment across the flume. Water velocity was maintained at 0.10 m·s^{-1} during all experimental trials.

In this study, a homogeneous sediment standard was applied to all experiments, one with relevance to natural sediment to which eggs and sperm may be exposed. All experiments used commercial clay derived from natural illite, ball clay, and kaolinite deposits (Plainsman H550; Plainsman Clays Ltd., Medicine Hat, Alberta) consisting of >90% silt and clay-size particles by weight (those <0.062 mm diameter; Wentworth 1922). Because physical sediment characteristics (size and angularity) have been correlated with differing degrees of detrimental effects on fish (e.g., Servizi and Martens 1987, 1991) and natural sediments collected from riverbeds or stream banks could potentially introduce uncontrolled factors such as sediment-bound contaminants (e.g., heavy metals or large organic molecules; Qiao and Farrell 1996; Lake and Hinch 1999), sediment composition and concentration was standardized across experiments by exclusive use of the Plainsman clay. The sediment in this study is similar in terms of particle size fractions (i.e., mostly silt and clay-sized particles similar to those that salmon may encounter) to that generated by placer mining operations and is identical to sediment used in other experiments (J.S. Korstrom, Fisheries and Oceans Canada, West Vancouver Laboratory, West Vancouver, BC V7V 1N6, personal communication) designed to emulate suspended sediment impacts on fish. Smaller size fractions are more likely to enter and remain in suspension and thus are more likely to be the size class of suspended particles that fish encounter (Caux et al. 1997).

Sediment slurries were created for each suspended sediment treatment by mixing different amounts of the powdered clay (0, 30, 75, 300, 1500, or 1600 g) in a bucket with 15 L of creek or lake water. These slurries would later be used by adding 3 L from a bucket to the flume for each trial. Buckets were placed in a shallow part of the stream to maintain bucket water temperature near stream temperature (14–15 °C). Water temperature in the flume trials never exceeded 15.5 °C. In both years, creek or lake water with ambient suspended sediment concentrations of less than 5 $mg \cdot L^{-1}$ was used for a control, though during experimentation, some residual particles remained in the flume from one trial to the next. This is evidenced by control values that were above the ambient suspended sediment concentrations (Table 1) and by visual observations of larger sediment particles remaining in the flume apparatus. Even so, relative to the magnitude of treatment concentrations, control values were small and had comparatively little variation. Nominal concentrations were identified for the first trials, but because of settling of the slurries, the actual sediment concentrations measured in the flumes were used. Suspended sediment values among treatment concentrations were well regulated; replicates within each sediment treatment had a coefficient of variation ranging from 5.7% to 16.4% (mean 10.5%).

Flume fertilization procedure

For each suspended sediment treatment, sediment slurries in the buckets were vigorously mixed to resuspend any settled sediment and then 3 L was added to the trough before the water pump was started. As the suspended sediment concentration equilibrated for a minimum of 1 min in the flume, eggs were weighed into an open-top brass wire cage (2 mm grid size) and milt was drawn into three 1 mL syringes. The syringes were then placed into a holder fitted to the flume immediately upstream and against the egg cage, a measure which ensured a consistent distribution of sperm over the eggs. Gametes in all trials were handled consistently and minimally.

In 1999, three syringes with 0.5 mL milt each and 21 g of eggs (approximately 200 in number) were used for each trial. Before the 2000 trials, it was determined that adequate fertilization at control concentrations of sediment could be achieved with less milt (0.33 mL per syringe) and fewer eggs (11 g or approximately 110 eggs), producing a higher milt to egg ratio (R.V. Galbraith, unpublished data). This allowed for more replication with the available gametes.

Before each fertilization trial, a water sample was taken from the flume for analysis of suspended sediment concentration. Total suspended sediment concentrations, as described by Caux et al. (1997), were determined for each experiment using procedures from the American Public Health Association (1995). At the end of each trial, the flume was emptied and thoroughly rinsed with clear water to remove as much remaining sediment as possible. Conductivity and pH values of water samples from different treatment levels ranged from 90 to 241 µS and 7.6 to 8.2, respectively. In comparison, ambient Kynoch Creek conductivity and pH values were similar and ranged from approximately 50 to 200 µS and 7.0 to 8.0, respectively (Herb Herunter, Fisheries and Oceans Canada, Simon Fraser University, School of Resource and Environmental Management, Burnaby, BC V5A 1S6, unpublished data).

To begin the trial, the egg cage was placed in the flowing water of the flume. Each syringe plunger was simultaneously drawn up to the 1.0 mL mark with flume water to dilute and activate sperm and then was pushed down at a steady rate. This procedure discharged the sperm upstream of the egg cage so that the flow of water would carry the sperm through and over the eggs. The entire process from egg contact with the flume water to completion of milt discharge took less than 7 s. After milt discharge, eggs remained in the flume for 30 s and then were removed, rinsed, and placed in a 500 mL jar filled with clean water to water harden for a minimum of 30 min.

Egg incubation

In the field study, 50–70 eggs were counted into perforated stainless steel cylindrical incubation capsules (3.7 cm × 12 cm with a tight-fitting test cap) yielding two to four capsules per trial. The eggs were dispersed among presorted gravel, 1.3 to 5.1 cm in diameter, added to each capsule to simulate redd incubation conditions (Scrivener 1988; Herunter et al. 2000; Patterson 2004). Capsules were buried at random within artificial redds in the stream at natural sockeye redd depths of 20–25 cm deep (Macdonald 1994). While spawning sockeye salmon were in the area of the artificial redds, a 2.5-inch wire fence surrounding the buried capsules prevented them from being disturbed. The fence was removed when adult sockeye were no longer present. Two standpipes placed at the same depth as the egg capsules were used to monitor intergravel water temperature and dissolved oxygen levels throughout the incubation; temperatures in both standpipes were identical to ambient stream temperature, and dissolved oxygen remained greater than 91% saturation. Capsules were removed after a minimum of 38 days incubation in 1999 and 47 days in 2000, once the eyed stage (Velsen 1980) could be easily distinguished visually. Fertilization success was determined as the percentage of eyed eggs to total eggs in the capsules from each trial. Eggs that had died or were alive but not eyed were considered unfertilized.

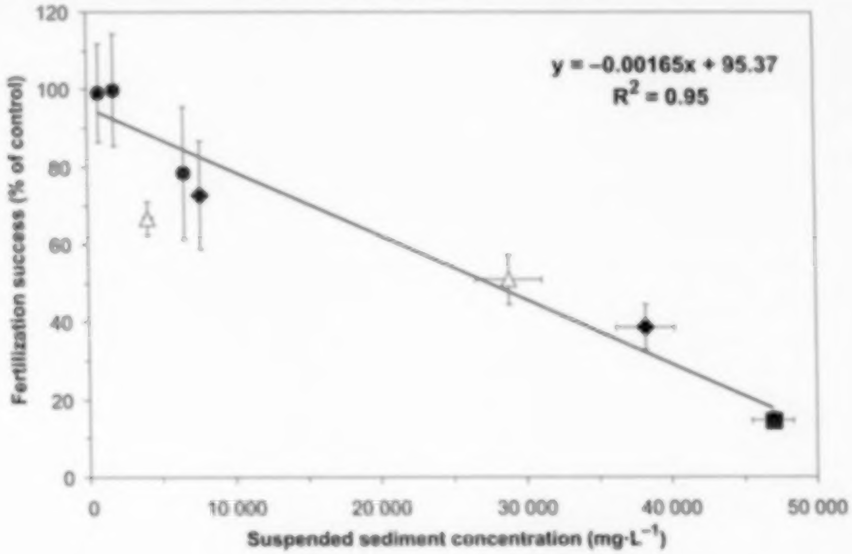
In the laboratory study, coho salmon eggs from each trial were counted into an incubation basket and placed in a Heath tray for 50 days, at which point the eyed stage (Velsen 1980) could be easily distinguished visually; they were then removed and counted. Fertilization success for each basket was determined as above.

These incubation methods have been shown to have >90% survival under optimal conditions (Herunter et al. 2000; Patterson 2004).

Dry fertilization procedure

Preliminary experiments demonstrated that controlling for gamete quality is an important consideration. To examine the variability between different pools or pairs of gametes in their ability to fertilize, a series of dry fertilizations, where sperm were mixed in a dish with eggs followed by water

Fig. 1. The relationship between egg fertilization success and suspended sediment concentration for sockeye salmon (*Oncorhynchus nerka*) (1999, ●; 2000 pooled, ■; 2000 paired, ◆), with coho salmon (*O. kisutch*; △) included for comparison. Experimental data are plotted as percentage of the control mean for each pool or pair of gametes in each experiment. Error bars are ± standard error.



(Scott and Baynes 1980; Herunter et al. 2000), were conducted to determine the fertilization success under optimal conditions (Patterson et al. 2004). This also allowed assessment of any decline in gamete viability over time in all groups of eggs and milt and comparison of the results to the flume fertilization trials.

Data analysis

All fertilization data were arcsine square-root transformed before statistical analysis. Values are reported as mean ± SE (standard error calculated for arcsine square-root transformed data and then upper and lower bounds were back-transformed to percentages) for replicate trials. Experimental results for individual experiments were analyzed with Minitab statistical analysis software (version 13.1; Minitab Inc., State College, Pennsylvania) using analysis of variance (ANOVA, $P \leq 0.05$) or, where there were different gamete groups used within an experiment, two-factor analysis of variance to test the hypothesis that the mean fertilization success was the same for all groups. When differences were detected, a Tukey–Kramer HSD (honestly significant difference) test was performed to identify significantly different groups.

Results

Egg fertilization success with the dry fertilization technique was used to measure the overall viability of each gamete pool or pair. The 1999 pooled sockeye salmon gametes had a dry fertilization success ranging from 92% to 98%, and the 2000 pooled sockeye salmon experiment had only one pool of milt and eggs with a fertilization success of 95%. In both cases, all data were used. However, some gamete pools or pairs were of poor quality, as determined by their success with the dry fertilization technique, and these data were therefore discarded and not included in the analysis. Five of the eight sockeye gamete pairs used in 2000 had dry fertilization results ranging from 87% to 96%, with the three remaining pairs (used in six trials for each treatment) fertilizing 19%, 32%, and 48% of eggs. These three pairs were removed from the remainder of the analysis. Of the two coho salmon gamete pools used, one had dry fertilization success of 98%, whereas the other had only 54%. This latter pool (used in five trials for each treatment) also showed essentially no fertilization in the water flume and so was removed from the analysis. In a further three coho salmon trials, a fungal infection contracted during incubation resulted in complete mortality of the eggs, and therefore, these data were also discarded. There was no indication in any experiments of declining viability from gamete harvest to fertilization.

Experiments conducted in the flume showed that there were significant differences in fertilization success between many of the gamete pools or pairs regardless of sediment concentration. For example, the 1999 pooled sockeye salmon experiment had no difference in fertilization success between pools of eggs, but there was a difference in milt quality, with each pool of milt fertilizing significantly different proportions of eggs ($P < 0.0001$). The paired gametes in 2000 also exhibited a significant difference in their fertilization success between the most successful pairing and the remaining gamete pairs ($P = 0.002$). This made it necessary to adjust for between-pool or -pair differences in fertilization success when comparing experiments, and so results from each fertilization trial are also expressed as a percentage of the control mean for that sockeye or coho gamete pool or sockeye gamete pair (Table 1; Fig. 1).

For Early Stuart sockeye salmon, we fit a linear regression model between suspended sediment concentration and fertilization success (Fig. 1). Using this model, with increasing concentration of suspended sediment, there is a downward trend in the proportion of eggs successfully fertilized (R^2 = 0.95). For comparison, the data generated in the laboratory with coho salmon are also included in Fig. 1.

Despite the strength of the empirical relationship in Fig. 1, statistical significance in individual experiments only occurs between the control and the highest sediment concentration treatments, with the exception of the 1999 pooled sockeye experiment (Table 1). Large variability in egg fertilization results, even for trials conducted at the same sediment concentration, meant that statistical significance was only detected for the largest differences in fertilization success. With sockeye salmon in 1999, the sediment concentrations were not high enough to cause a detectable effect; however, the mean percent fertilization success did decline to 78.4% of control values at a mean suspended sediment concentration of 6621 ± 120 $mg \cdot L^{-1}$ ($P = 0.267$). In 2000, the pooled gamete experiment used a higher concentration of suspended sediment (46 943 ± 1412 $mg \cdot L^{-1}$), and this resulted in a significant effect on fertilization success when compared with its control ($P < 0.001$). For the paired gametes, the difference in fertilization success was significant in comparisons between the control and the 38 231 ± 1987 $mg \cdot L^{-1}$ sediment concentration ($P < 0.001$), with the lower sediment treatment (7691 ± 278 $mg \cdot L^{-1}$) not statistically different from the control ($P = 0.091$). In the laboratory study using coho salmon, there was again a significant difference in fertilization success between the control and the highest sediment treatment (28 835 ± 2263 $mg \cdot L^{-1}$, $P = 0.027$).

Discussion

According to the linear model of suspended sediment effects on fertilization success in sockeye salmon, decreases in salmon fertilization success that could influence fisheries management decisions (e.g., 10% to >20% reduction in the proportion of eggs successfully fertilized) may occur at mean suspended sediment levels ranging from 3300 to >9300 $mg \cdot L^{-1}$. As a comparison, Newcombe and Jensen's (1996) severity-of-ill-effect model for adult salmon predicts that short-term exposure (up to 24 h) to elevated suspended sediment levels in this range may elicit major physiological stress and some mortality. The suspended sediment – egg fertilization empirical relationship suggests that salmon spawning during such an event could suffer from substantial impacts to the proportion of eggs successfully fertilized. Though salmonids may be unlikely to remain in an area with such elevated suspended sediment concentrations (Servizi and Martens 1992), an avoidance response may not always be possible or immediate, especially during acute suspended sediment events. In this case, the model implies that high suspended sediment concentrations are likely to have significant impacts on the fertilization and reproductive success of sockeye salmon incremental to detrimental effects on adults and egg incubation habitat due to sediment exposure. Coho salmon also exhibited a comparable effect of suspended sediment on their fertilization success.

Overall, the suspended sediment concentration at which egg fertilization success is impacted was above levels that typically require preventative or mitigative management action. Most guidelines to protect aquatic life from suspended sediment suggest that concentrations above 400 $mg \cdot L^{-1}$ warrant serious concern, and if background levels are above this range, then an acceptable maximum increase from that point is 10% of the background concentration (European Inland Fisheries Advisory Commission 1964; Canadian Council of Resource and Environmental Ministers 1987). This range is considerably less than values modeled in this paper for impacts on sockeye salmon fertilization success, where suspended sediment levels are approaching concentrations where lethal effects on adults and juveniles are likely to take place (Birtwell 1999; Newcombe and Jensen 1996).

An effect of suspended sediment on the fertilization process has not previously been demonstrated, though perhaps it is expected. In general, the effect of suspended sediment on aquatic organisms is a function of both concentration and duration of exposure (Newcombe and Jensen 1996). However, duration of exposure is extremely brief in the case of impacts on individual salmon spawning events and egg–sperm interaction. Because the period of elevated suspended sediment events can last hours or days and the entire fertilization event lasts only seconds, exposure duration is irrelevant when fertilization takes place. Any suspended sediment interference in the fertilization process must occur between gamete release and fertilization. In effect, this means that the concentration, not the duration, of suspended sediment exposure is the primary variable of interest when investigating potential impacts on fertilization. In the present study, sperm release was simulated using syringes, while maintaining a constant suspended sediment concentration and water flow that was comparable to natural water velocities preferred by spawning sockeye salmon (Lorenz and Eiler 1989). Moreover, the fertilization was likely completed in less than 10 s (Hoysak and Liley 2001).

Timing is a critical factor in fertilization success. The majority of salmonid eggs are fertilized less than 10 s after gamete release (Liley et al. 2002), and in fact, gamete viability is severely reduced 20 s after release into water (Hoysak and Liley 2001; R.V. Galbraith, unpublished data). Stuart (1953) demonstrated that silt can adhere to the salmonid egg surface, and Billard and Cosson (1992) estimated that for successful fertilization to occur within the active life of a sperm, it would have to be released in close proximity to the micropyle of the egg. Therefore, it is clear that sperm have a limited time frame and distance to successfully fertilize eggs and suspended sediment particles that interfere with sperm–egg micropyle contact could result in impaired fertilization success.

It is unknown whether the decrease in the proportion of successfully fertilized eggs observed was due to direct sediment particle effects on sperm mobility and sperm–micropyle encounter rates or due to sediment particles coating and blocking the micropyle. In this study, the sediment size fractions of the Plainsman clay were very small, with the majority of the particles less than 0.062 mm in diameter (silt and clay classification) and of these >40% were less than 0.002 mm. The inner aperture of the egg micropyle and head of the sperm cell are also 0.002 mm (Yanagimachi et al. 1992), thus there is potential for the micropyle to be plugged or blocked to sperm entry by these small sediment particles, and the higher the suspended sediment concentration, the greater is the probability of sediment particle – egg micropyle encounter.

Though we monitored water quality characteristics during this study (pH, conductivity, temperature) and they were not different from ambient creek values, it is possible that suspended sediments could change other water quality characteristics outside of these. However, these effects may be difficult to identify as they would co-occur with any physical consequences and would likely be buffered by the presence of ovarian fluid in the natural spawning environment (Woolsey et al. 2006).

The dry fertilization technique is a best-case scenario for achieving fertilization success by providing optimum egg to sperm exposure. The dry fertilization technique procedures performed here achieved egg fertilization success near 90% or greater, which met or exceeded levels expected for healthy gametes combined using dry fertilization methods (Billard 1992; Patterson et al. 2004). In-flume control fertilizations in the experiment were often less than half of this. Though it may be assumed that fertilization trials performed in the flume would be less successful, presumably because gametes in flowing water have less time for egg–sperm contact and exposure to water before eggs are fertilized reduces gamete viability (Hoysak and Liley 2001; R.V. Galbraith, unpublished data), natural spawning success in the wild is relatively unknown but, in some cases, has been reported to be extremely high, with values in some cases approaching 95% or greater (Mathisen 1962; Egorova 1970). However, the conditions under which natural spawning takes place are difficult to replicate, and though the flume water velocities were within the range of velocities preferred by most salmon (0.10–$0.15\ \mathrm{m \cdot s^{-1}}$; Lorenz and Eiler 1989), the environment was not entirely representative of the true conditions created by a redd. A salmon redd creates a pocket of low to no water flow in order to maximize fertilization success (Sandercock 1991), and neither flume contained any such pocket. Indeed, creating and maintaining such a low flow arrangement would have been problematic to sustaining consistent suspended sediment concentrations. This discrepancy can describe, in part, why the in-flume control fertilizations, though taking place under conditions that are more comparable to those of natural fertilization events in the wild than the dry technique, had less success than that found in natural, wild fertilization events (in-flume mean control range 35.3%–61.4% versus >95%).

This study demonstrated an effect of suspended sediment concentration on the proportion of successfully fertilized eggs in salmon. Indeed, it is the first work to utilize a method of experimentally fertilizing gametes in flowing water. Fisheries and fish habitat management decisions and impact assessments involving salmon and suspended sediment interactions currently take into account potential influences on salmonid adults, juveniles, incubating eggs, and embryos. It has been shown here that suspended sediments can also have a significant, negative influence on egg fertilization success, albeit at a concentration well above what fish may be exposed to under normal spawning conditions. The concentration of suspended sediment that elicits a change in fertilization success may differ with salmon stocks or species, sediment particle size and angularity, and water conditions. The suspended sediment range tested and the resultant empirical model can be used as a guide for concentrations to be tested in future work, though as discussed, differences between the experimental conditions created in the flume and the natural spawning environment must also be considered. Nevertheless, in the absence of other experimental information, the negative relationship between suspended sediment concentration and fertilization success derived herein provides a preliminary guideline for evaluating impacts on spawning success, and the effect of suspended sediment on egg fertilization in salmon should be added to the list of likely consequences associated with increased suspended sediments in aquatic habitats.

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Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska

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Abstract: Steller sea lions (*Eumetopias jubatus*) increased in the eastern portion of their range while declining in the Gulf of Alaska and Aleutian Islands from the late 1970s to late 1990s. We constructed ecosystem models of the central and western Aleutians and of southeast Alaska to simultaneously evaluate four hypotheses explaining sea lion dynamics: killer whale (*Orcinus orca*) predation, ocean productivity, fisheries, and competition with other species. Comparisons of model predictions with historical time series data indicate that all four factors likely contributed to the trends observed in sea lion numbers in both ecosystems. Changes in ocean productivity conveyed by the Pacific Decadal Oscillation influenced the abundance trajectory of several species. Fishing could have affected the ecosystem structure by influencing the abundance of Atka mackerel (*Pleurogrammus monopterygius*) in the Aleutians and Pacific herring (*Clupea pallasii*) in southeast Alaska. Pacific halibut (*Hippoglossus stenolepis*) in the Aleutians and arrowtooth flounder (*Atheresthes stomias*) in southeast Alaska appear to impede sea lion population growth through competitive interactions. Predation by killer whales was important when sea lions were less abundant in the 1990s in the Aleutians and in the 1960s in Southeast Alaska, but appear to have little effect when sea lion numbers were high.

Résumé : La population d'otaries de Steller (*Eumetopias jubatus*) a augmenté dans le sud-est de l'Alaska tandis qu'elle a décliné de façon dramatique dans le Golfe de l'Alaska et les Iles Aléoutiennes, de la fin des années 1970 jusqu'à la fin des années 1990. Nous avons construit des modèles d'écosystème des Iles Aléoutiennes (centre et ouest) et du sud-est de l'Alaska pour examiner simultanément quatre hypothèses: la prédation par les orques (*Orcinus orca*), la productivité océanique, la pêche, et la compétition avec d'autres espèces. La comparaison des prédictions du modèle et des séries temporelles indique que ces quatre facteurs ont vraisemblablement contribué aux variations d'abondance des otaries dans les deux écosystèmes. Les changements de productivité océanique, représentés par l'oscillation pacifique décennale, ont influencé l'abondance de plusieurs espèces. La pêche semble avoir affecté l'écosystème en influençant l'abondance du maquereau d'Atka (*Pleurogrammus monopterygius*) dans les Aléoutiennes et du hareng du Pacifique (*Clupea pallasii*) dans le sud-est de l'Alaska. La compétition avec le flétan du Pacifique (*Hippoglossus stenolepis*) dans les Aléoutiennes et la plie à grande bouche (*Atheresthes stomias*) dans le sud-est ont contribué au ralentissement de la croissance de la population d'otaries. La prédation par les orques s'est avérée être un facteur important lors des faibles abondances des populations d'otaries, soit dans les années 1990 dans les Aléoutiennes et dans les années 1960 dans le sud-est. La prédation a par contre peu d'effet lorsque les otaries sont abondantes.

Introduction

Steller sea lions (*Eumetopias jubatus*) declined by more than 80% in the western Gulf of Alaska (GOA) from the late 1970s to the late 1990s (Merrick et al. 1987; Trites and Larkin 1996; Calkins et al. 1999). In contrast, the population in southeast Alaska (SE Alaska) and British Columbia (B.C.) have increased during the same period (Calkins et al. 1999). Various hypotheses have been formulated to explain the decline (DeMaster and Atkinson 2002; National Research Council 2003), but none have been put forward to explain the increase of sea lions in SE Alaska.

Three of the leading hypotheses to explain the decline in the western GOA are predation, change in oceans productivity, and fishing. The first of these proposes that the decline may be related to predation by transient killer whales (*Orcinus orca*) in the western GOA (Heise et al. 2003; Springer et al. 2003; Williams et al. 2004). The second hypothesis is that the carrying capacity for sea lions was reduced by a decrease in primary production in the western GOA because of a shift in ocean climate that occurred in 1977, altering the quantity and (or) the quality of the food web (Merrick et al. 1997; Anderson and Piatt 1999; Trites et al. 2006*c*). The third hypothesis is that the large-scale fisheries in the GOA modified the ecosystem structure and function to the detriment of sea lions (Alverson 1992; Hansen 1996; Trites and Donnelly

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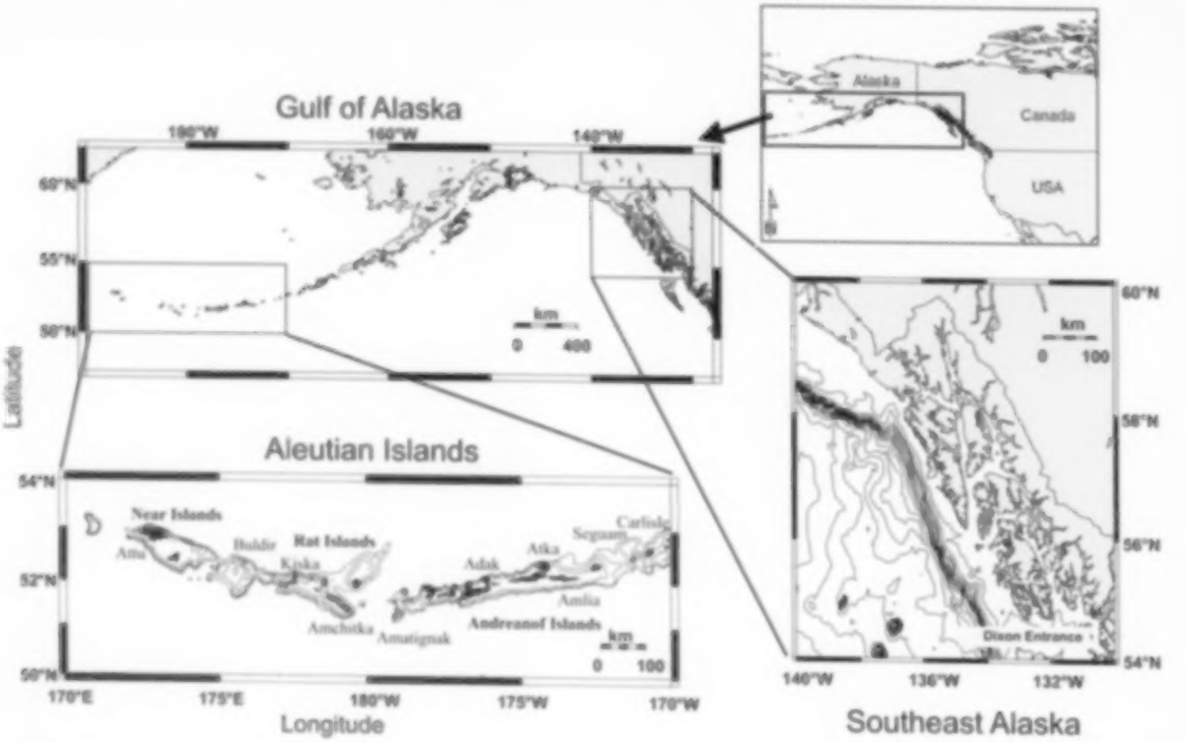
Fig. 1. Location of the two study areas, Southeast Alaska and the central and western Aleutian Islands.



2003). Another possible explanation is that sea lions are unsuccessfully competing with other species (Trites et al. 1999; Aydin 2002). Most of the research conducted to date into the reasons for the decline of the western population of Steller sea lions has attempted to test only one hypothesis at a time.

The objective of our study was to examine the combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions in the western GOA using ecosystem modelling. We employed a widely used ecosystem modelling approach, Ecopath with Ecosim (EwE, www.ecopath.org; Christensen and Walters 2004). We also sought to gain insights in the population decline in the Aleutian Islands by examining reasons why the SE Alaska population might have increased. We therefore compared two contrasting study areas that differed by the trends of their respective sea lion populations, their fishing histories, and the characteristics of their ecosystems: the western and central Aleutian Islands (henceforth simply referred to as the Aleutian Islands) and SE Alaska (Fig. 1). We modelled the period 1963–2002, which encompasses the ocean regime shift, the development of the major fisheries, and the major changes in Steller sea lion abundances.

Materials and methods

Study area

The Aleutian Islands of our study are contained within 170°E and 170°W, to the 500 m depth contour, for a total area of 56 936 km^2 (Fig. 1). The eastern cutoff point was Carlisle Island, which meant that the region did not include Unimak Pass, a known aggregation area for marine mammals. The SE Alaska study area consisted of the continental shelf east of 140°W to 1000 m depth and included the eastern part of the Yakutat region (140°W–137°W) and the coastal region east of 137°W. The southern limit was the border between B.C. and Alaska (Dixon Entrance).

The Aleutian Islands are characterized by a narrow shelf and very few rivers able to sustain salmon species (*Oncorhynchus* spp.). The area is currently characterized by a large biomass of Atka mackerel (*Pleurogrammus monopterygius*) that is commercially fished. In contrast, SE Alaska is characterized by a large number of rivers that are important for salmon species, as well as for its large population of Pacific herring (*Clupea pallasii*) and many species of rockfish (*Sebastes* spp.). The most important species for evaluating the hypotheses are transient killer whales, Steller sea lions, Atka mackerel, salmon, Pacific herring, arrowtooth flounder (*Atheresthes stomias*), and Pacific halibut (*Hippoglossus stenolepis*). Parameters for these species are described in detail below.

The model

Ecosystem models account for the biomass (t·km^{-2}) of each functional group (composed of a single species or a group of species), their diet composition, consumption per unit of biomass, natural and fishing mortality, accumulation of biomass, and net migration. The principle behind this ecosystem modelling approach is that biomass and energy are conserved on a yearly basis (Walters et al. 1997). Ecosim is a tool for dynamic simulations based on the Ecopath model, an instantaneous image of the ecosystem in time. Ecosim uses a system of differential equations to describe the changes in biomass and flow within the system over time by accounting for change in predation, consumption rate, and fishing (Walters et al. 1997; Christensen et al. 2005). Thus, the rate of change of biomass of group i (B_i) is described by

$$\text{(1)} \qquad \frac{\mathrm{d}B_i}{\mathrm{d}t} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (m_i + F_i + e_i)B_i$$

where g_i is the net growth efficiency; Q_{ji} and Q_{ij} are the consumption rate of group j by group i and the consumption of group i by group j, respectively; I_i is the immigration flow in $\mathrm{t \cdot km^{-2}}$; m_i is non-predation mortality; F_i is fishing mortality; and e_i is emigration rate (Christensen and Walters 2004).

EwE allows the fitting of time series of abundance and thus a comparison of how the model replicates observed behaviour through time. Ecosim is also able to incorporate multiple stanzas representing life history stages for species with complex life histories (sea lions and walleye pollock (*Theragra chalcogramma*) in these models). The stanzas are linked and their respective production per unit of biomass (*P*/*B* per year), consumption per unit of biomass (*Q*/*B* per year), and growth are calculated from a baseline estimate for a leading group (the adults in our case). Growth for each stanza is calculated following the von Bertalanffy growth curve and assuming stable survivorship through ages (Christensen et al. 2005).

The functional predator–prey relationship is based on the foraging arena theory, dividing the prey biomass into vulnerable and invulnerable pools (Walters and Kitchell 2001). The transfer rate between these two pools (also called vulnerability) can range from 0 to ∞, with higher rates implying that the behaviour of both the prey and the predator have weaker effects on limiting predation rates. A large vulnerability value also means that the predator initial biomass is low compared with its carrying capacity and that a change in its biomass will cause a corresponding change in the mortality rate of its prey. The system will thus be more stable when a predator is close to its carrying capacity and more variable when far from it. Vulnerability values can be specified for each predator–prey pair. Owing to uncertainties in how this parameter might change among prey species and notably to reduce the number of parameters that needs to be estimated, we chose to assume that the vulnerability setting is the same for all species of prey that a given predator consumes.

This functional predator–prey response equation predicts changes in diet composition due to changes in relative availability of prey and alternative prey, but it does not allow switching of the diet to new prey that were not consumed initially. In Ecosim, the predator can follow a type II functional response (Holling 1959), in which a prey consumption increases with prey abundance until an asymptote is reached. A type II functional relationship supposes that killer whales are able to maintain their rate of predation on sea lions as abundance declines by using other mammals as well. A type III functional relationship is due to the predator changing prey types as its preferred prey reaches a low level. In Ecosim, the addition of the foraging arena model can also produce a type III functional response, because at low density the prey will change its behavior and be less accessible to predation.

In addition to vulnerability, consumption is governed by limitations placed on predator consumption rates by foraging time adjustments, maximum relative feeding time, and handling time effects (Walters and Martell 2004; Christensen et al. 2005). The time that a predator spends foraging increases as relative prey availability diminishes. This in turn results in greater exposure and greater risk of the predator itself being eaten. The feeding time adjustment factor determines how fast individuals adjust their feeding times. A value of 0 causes feeding time to remain constant, with all changes in relative food availability being channelled to changes in growth rate. A value of 1 results in a fast time response, less predation risks, and a lesser growth rate. In our models, the feeding adjustment time was set to 0.5 for marine mammals, except for sea lion pups and embryos, and was 0 for other species (assuming that large predators are more likely to vary their feeding search time as food availability changes). As a rule, the maximum relative feeding time was not allowed to increase more than twofold (Christensen et al. 2005). Killer whales have no predators and were allowed to increase their maximum feeding time to 10 instead of 2 times the initial value, and the fraction of total mortality sensitive to predation mortality was set at 0.2. The handling time parameter was left at default values, assuming that the limitations imposed by the vulnerability values were sufficient. The relative foraging time factors were evaluated iteratively at each monthly time step (Walters and Martell 2004, p. 242).

Model fitting was achieved by evaluating vulnerabilities that minimized the sum of squares of differences between model predictions and the catch and biomass time series data. In addition, indices of climate changes were added to modify primary production.

We forced the model to fit the catches for groups without reliable biomass or fishing mortality series (toothed whales, mammal-eating sharks, salmon, large demersal, sablefish (*Anoplopoma fimbria*), and Pacific halibut in the Aleutians; toothed whales, small mammals, sea otters (*Enhydra lutris*), sharks, slope rockfish, walleye pollock, and flatfish in SE Alaska). Using a stock reduction analysis (Kimura 1985), historical catches were treated as fixed, known quantities and were subtracted from simulated stock size over time so as to aid in estimating how large (and (or) productive) the stock must have been to sustain those catches. Given the production of the stock and the catch time series, the model estimated the minimum biomass necessary for fisheries and predators' needs. Catches were sometimes forced for only part of the time series, typically for the beginning of the time series.

Data

The ecosystem models were initialized in 1963 and comprised 39 functional groups, with 9 groups of marine mammals and 21 groups of fish (Table 1). Commercially important species were considered separately in the models to ensure that fisheries were accounted for adequately. The structure of the models reflected the goals of our study. Thus we explicitly considered Steller sea lions, their predators,

Table 1. Functional groups description and parameters used for the balanced and fitted Aleutian Islands and Southeast Alaska models.

Group	Species	Aleutians Biomass (t·km⁻²)	Aleutians *P/B* (year⁻¹)	Aleutians *Q/B* (year⁻¹)	Aleutians EE	Aleutians BA (year⁻¹)	Aleutians Vuln.[c]	Southeast Alaska Biomass (t·km⁻²)	Southeast Alaska *P/B* (year⁻¹)	Southeast Alaska *Q/B* (year⁻¹)	Southeast Alaska EE	Southeast Alaska BA (year⁻¹)	Southeast Alaska Vuln.[c]
Transient killer whales	Mammal-eating *Orcinus orca*	0.0006	0.025	10.8	0	—	>100	0.0007	0.02	11	**0**		>100
Toothed whales	*Physeter catodon* and fish-eating *Orcinus orca* and beaked whales in the Aleutians	0.013	0.036	11.1	0.95	−0.03	1	0.0175	0.03	11.5	**0.05**	−0.03	1.03
Baleen whales	*Balaenoptera physalus*, *Balaenoptera borealis*, *Megaptera novaeangliae*, *Balaenoptera acutorostrata* and *Eschrichtius robustus* and *Balaenoptera musculus* in the Aleutians	0.145	0.099	7	0.31	−0.02	>100	0.0361	0.099	10.9	**0.12**	−0.05	1.8
Steller sea lion	*Eumetopias jubatus*												
Embryo		**0.0001**	0.02	**220.8**	0	—	—	**2.39×10^{-6}**	0.02	**227.9**	**0**	—	—
Pup		**0.00202**	0.521	**83.4**	0.68	—	—	**0.0001**	0.59	**86.4**	**0.82**	—	—
Juvenile		**0.0301**	0.241	**39.6**	0.52	—	5	**0.00144**	0.19	**40.5**	**0.75**	—	1
Adult		0.148	0.174	25.6	0.11	—	25	0.013	0.11	25.5	**0.7**	—	1
Small mammals	Mainly *Phocoena vitulina* in Southeast Alaska and *Phocoenoides dalli* in the Aleutians	0.022	0.2	22.7	0.29	−0.01	3.85	0.041	0.21	28.85	**0.8**	—	1
Sea otter	*Enhydra lutris*	0.004	0.117	86.4	0.44	—	—	0.00003	0.21	85	**0.95**	0.2	65
Birds	All marine pelagic and coastal marine birds listed in Hunt et al. 2000	**0.00177**	0.113	65.4	0.95	—	—	0.006	0.38	68	**0.39**	—	—
Mammal-eating sharks	*Somniosus pacificus*, *Carcharodon carcharias*, and *Hexanchus griseus*	0.05	0.125	**0.6**	**0.43**	—	1	0.01	0.13	**1.3**	**0.07**	—	—
Sharks and skates	Mainly *Lamna ditropis*, *Squalus acanthias*, *Raja binoculata*	2.6	0.159	**0.8**	**0.15**	—	2.57	0.25	0.12	**1.2**	**0.71**	—	—
Salmon	*Onchorhynchus gorbuscha*, *Onchorhynchus kisutch*, *Onchorhynchus keta*, *Onchorhynchus tshawytscha*, *Onchorhynchus nerka*	**1.162**	1.168	4.3	0.5	—	1	1.11	2.1	**10.5**	**0.35**	—	1.1
Pelagic, large	Includes *Mola mola*, *Trachipterus altivelis*, *Merluccius productus*	**0.004**	0.22	1.5	0.95	—	—	**0.034**	0.22	**1.1**	0.95	—	—

Table 1 *(continued)*.

		Aleutians						Southeast Alaska					
Group	Species	Biomass (t·km^{-2})	*P/B* (year^{-1})	*Q/B* (year^{-1})	EE	BA (year^{-1})	Vuln.[c]	Biomass (t·km^{-2})	*P/B* (year^{-1})	*Q/B* (year^{-1})	EE	BA (year^{-1})	Vuln.[c]
Pelagic, small	*Mallotus villosus*, Osmeridae, *Engraulis mordax*, *Scomber japonicus*	**2.723**	0.8	3.6	0.95	—	—	**0.91**	0.89	**4.45**	0.95	—	—
Atka mackerel[a]	*Pleurogrammus monopterygius*	13.5	0.34	**1.7**	**0.99**	—	1.1					—	—
Sand lance	*Ammodytes hexapterus*	**0.779**	0.8	3.6	0.95	—	—	1.3	1.15	**5.75**	**0.58**	—	—
Pacific herring	*Clupea pallasii*	**2.771**	0.16	1	0.95	—	1.21	0.345	1.27	**6.35**	**0.83**	-0.15	25
Walleye pollock	*Theragra chalcograma*												
Juvenile		**0.67**	1.2	**4.7**	**0.78**	—	—	**0.005**	1.2	**5.9**	**0.88**	—	—
Adult		6.08	0.304	2	**0.99**	—	1	0.2	0.3	1.5	**0.87**	0.02	>100
Pacific ocean perch	*Sebastes alutus*	1.1	0.068	**0.7**	**0.94**	—	5	2.38	0.07	**0.35**	**0.78**	—	1.31
Rockfish, slope	Mainly *Sebastes aleutianus*, *Sebastes borealis*, *Sebastes flavidus*, *Sebastes polyspinus*, *Sebastolobus* sp.	**1.23**	0.1	**1**	0.95	—	1	**0.68**	0.11	**0.54**	0.95	—	—
Rockfish, shelf[b]	Mainly *Sebastes ruberrimus*	—	—	—	—	—	—	**2.62**	0.02	**0.11**	0.95	—	—
Sablefish	*Anoplopoma fimbria*	1.8	0.106	1	**0.49**	-0.02	>100	0.89	0.13	**0.65**	**0.67**	0.03	1.24
Pacific cod	*Gadus macrocephalus*	2.4	0.37	2.3	**0.55**	0.03	1.1	0.28	0.37	**1.85**	**0.91**	0.02	2
Pacific halibut	*Hippoglossus stenolepis*	**0.4**	0.19	**1.3**	0.9	0.03	25	0.28	0.36	**1.8**	**0.91**		1
Arrowtooth flounder	*Atheresthes stomias*	0.5	0.3	**2**	**0.6**	—	1	0.5	0.2	**1**	**0.98**	0.03	>100
Demersal, large	Species from 20 to 240 cm, including *Myoxocephalus polyacanthocephalus*, *Hydrolagus colliei*, *Anarrhichthys ocellatus*, etc.	**3.26**	0.4	2	0.95	—	—	**0.197**	0.27	**1.34**	0.95	—	—
Flatfish	All soles and flounder	**2.83**	0.188	1.7	0.5	—	—	**1.76**	0.263	**1.3**	0.95	—	—
Demersal, small	Species smaller than 62 cm; Hexagrammids, Liparidae, Zoarcidae, Cottidae, Agonidae	**5.1**	0.6	3	0.95	—	—	**0.99**	1.07	**4.3**	0.95	—	—
Deepwater, large	Grenadiers, lancetfishes, rattails, eels	**0.49**	**0.4**	2	0.95	—	—	**0.14**	0.45	**2.2**	0.95	—	—
Deepwater, small	Myctophidae and Bathylagidae	**7.6**	0.8	3.6	0.95	—	—	**1.33**	1	**4**	0.5	—	—
Shrimps	Commercially and noncommercially exploited	**3.22**	2.04	10.2	0.95	—	—	**2.53**	2	13	0.95	—	—

Table 1 *(concluded).*

		Aleutians						Southeast Alaska					
Group	Species	Biomass ($t\cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	BA ($year^{-1}$)	Vuln.[c]	Biomass ($t\cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	BA ($year^{-1}$)	Vuln.[c]
Benthic invertebrates	Ostracods, nematods, amphipods, coelenterates, noncarnivorous echinoderms	**26.21**	**2.529**	8.4	0.95	—	—	50	2	17	**0.27**	—	—
Epibenthic, carnivorous	Crabs, carnivorus echinoderms, and snails	**8.12**	1.283	5	0.95	—	—	**2.88**	1.3	**8.7**	0.95	—	—
Cephalopods	Octopuses and squids	**2.09**	2.94	7.2	0.95	—	—	**0.22**	2.55	10	0.95	—	—
Zooplankton, large	Mysids, chaetognaths, euphausiids, and jellyfishes	**14.08**	5.87	16	0.95	—	—	40	4.3	16.9	**0.82**	—	—
Zooplankton, small	Including calanoids	**9.4**	23.73	112.4	0.95	—	—	**17.15**	20	112	0.9	—	—
Phytoplankton		17.19	129.55	—	**0.37**	—	—	31.8	100	—	**0.74**	—	—
Marine plants	Macrophytes	**12.9**	8.12	—	0.1	—	—	23.23	4.4	—	**0.88**	—	—

Note: *P/B*, production per unit of biomass; *Q/B*, consumption per unit of biomass; EE, ecotrophic efficiency; BA, biomass accumulation rate; Vuln., vulnerability. Values estimated by Ecopath are in bold.

[a] Aleutians model only.

[b] Southeast Alaska model only.

[c] Lists vulnerability that were changed from the default value of 2.

and their principal prey species and only summarized the data that directly pertained to our objectives. Additional details about the models are given by Heymans (2005) and Guénette (2005).

Biomass estimates and time series generally came from stock assessment reports from the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADF&G) or as estimates from survey data provided by NMFS. Catch series were assembled from stock assessment reports and from data provided by ADF&G and NMFS. Time series of fishing mortality estimates were obtained from stock assessment or calculated from the catch/biomass ratio. Catch, biomass, and fishing mortality for the period 1963–2000 were assembled from stock assessment reports and related publications.

In some cases, it was necessary to attempt population reconstruction to estimate biomass from 1963 to 1977. In these cases, we used a simple Schaefer model:

$$(2)\qquad N_{t+1} = N_t + N_t r(1 - N_t/k) - C_t$$

where r is the intrinsic rate of growth, N_t is the abundance at time t, k is the carrying capacity, and C_t is the catch. The best solution, based on sum of squares, for k given a range of values of r and the initial abundance in the model time series (N_i) was found using the Solver routine in Microsoft Excel (Microsoft Corporation, Redmond, Washington).

For the Aleutians model, *P/B* and *Q/B* were generally obtained from a preliminary model developed at NMFS (Y. Ortiz, School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98115, USA). However, they were corrected or complemented according to the following methods, which were also used to estimate parameters for the SE Alaska model (see Table 1 for results). Consumption rates for mammals were based on energy requirements found in Perez and McAlister (1993) using the empirical equation $E = aM^{0.75}$, where E is the energy requirement per day ($kcal\cdot day^{-1}$; 1 calorie = 4.186 J), M is the mean body weight (kg), and a is a coefficient varying with the group of mammals (a = 320 for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). Direct ration estimates were used for sea lions (Winship and Trites 2003) and sea otters (Estes and Palmisano 1974). The average *Q/B* has been weighted by species biomass (see Table 1). Fish *Q/B* per year was typically calculated according to the empirical regression of Christensen and Pauly (1992):

$$(3)\qquad Q/B = 10^{6.37} \times 0.0313^{Tk} W_{\infty}^{-0.168} 1.38^{Pf} 1.89^{Hd}$$

where W_{∞} is the asymptotic body weight in grams, Tk is the mean annual temperature expressed as 1000/(T (°C) + 273.1), Pf equals 1 for predators and zooplankton feeders and 0 for all others, and Hd equals 1 for herbivores and 0 for carnivores. However, this method typically overestimated the consumption for long-lived fish (Guénette 2005), which was calculated instead using a production/consumption ratio of 0.2.

Fish natural mortality (M) was preferably taken from the literature (e.g., stock assessment reports) for commercial species. For other species, natural mortality was derived from the empirical model of Pauly (1980):

(4) $$M = K^{0.65} L_{\infty}^{-0.279} T^{0.463}$$

where K (year^{-1}) and L_{∞} (cm) refer to the curvature and asymptotic length parameters, respectively, of the von Bertalanffy growth function, and T is the mean annual water temperature (°C). Alternative estimates were taken from Hoenig's empirical equation (Hoenig 1983) for species that are not as well known:

(5) $$\ln(M) = 1.44 - 0.982\ \ln(\text{max age})$$

P/B values resulting for the sum of natural and fishing mortalities are listed in Table 1.

Fish diets obtained from NMFS for the Aleutian Islands were often specific for the area, while diet compositions for SE Alaska were generally taken from local or regional studies (for details see Guénette 2005; Heymans 2005). When necessary, diet data for the SE Alaska model were adapted from studies made in the central GOA and studies from the Hecate Strait (B.C.). For example, the Pacific halibut diet taken from the central GOA included a lot of walleye pollock, a species that is relatively less abundant in SE Alaska. Walleye pollock was partially replaced by sablefish based on observations by Sigler et al. (2002) and by Pacific herring, arrowtooth flounder, rockfish, and flatfish, prey that were shown to be used by Pacific halibut in the Hecate Strait (I. Pearsall and J. Fargo, Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9R 5K6, personal communication). The resulting diet matrices represented the 1980s and the 1990s, when most studies were carried out, and were modified to account for the changes in relative biomass between 1963 and the 1990s. For example, the proportion of Pacific herring in diets of fish and mammals of SE Alaska had to be decreased because the biomass of herring was too low to support all these species in 1963. Dietary proportions were therefore decreased for all predators but even more so for the predators that were responsible for a larger fraction of herring predation mortality. Changes to the diet were made on the basis of preserving diet preferences, not adding any new food items to counterbalance the decrease in biomass of an important food item. In the Aleutians, it was not necessary to modify the diet of arrowtooth flounder and Pacific halibut as it was in the SE Alaska model (Table 2). In the Aleutians, sea lion diet was modified by decreasing the proportion of Pacific halibut and Pacific ocean perch because the biomass of these prey species was lower in the 1960s. In SE Alaska, Pacific herring was replaced in the sea lion diet with salmon, rockfish, Pacific ocean perch, and sand lance (*Ammodytes hexapterus*).

Transient killer whales

Diets for transient killer whales, the ecotype of killer whale that eats only marine mammals, were inferred from observations reported in the literature as well as from stomach contents and visual observations of hunting behaviour and killings (Ford et al. 1998; Ford and Ellis 1999; Heise et al. 2003). Admittedly, these estimates may be biased by the different probabilities of observing any of these events for each prey species. Transient killer whales are assumed to feed primarily on small marine mammals (harbour seals (*Phocoena vitulina*), harbour porpoises (*Phocoena phocoena*), etc.), sea lions, and baleen whales (Table 2). Sea otters (*Enhydra lutris*) were included in the killer whales diet in the Aleutians based on recent observations (Estes et al. 1998; Doroff et al. 2003). To explore the possible impact of killer whales on Steller sea lions, we considered several scenarios about the proportion of sea lions consumed by killer whales in the Aleutians model.

Springer et al. (2003) assumed that 14 transient killer whales occur year-round in the western Aleutians (0.0006 t·km^{-2}). Alternatively, Fiscus et al. (1981) counted 63 killer whales in the central Aleutian Islands (from the Rat Islands to the Fox Islands). Assuming that 10% (six) of these 63 whales were transients (Waite et al. 2002) results in a total biomass of 0.0003 t·km^{-2}.

Of the 219 transient killer whales catalogued so far from Washington to SE Alaska, 6% have only been seen in SE Alaska, 50% have been seen in SE Alaska and B.C., and 44% in B.C. and Washington (Ford and Ellis 1999). Between 1984 and 2002, there have been 703 sightings of 137 different whales in SE Alaska (Straley et al. 2003). Thus, 133 transients were assumed to be present in SE Alaska during the 1990s. As transients are constantly travelling and may cover large distances within a month (Ford and Ellis 1999), we assumed that they stayed in SE Alaska for 2–3 months, which amounted to 26 whales year-round (0.0007 t·km^{-2}).

Steller sea lions

Steller sea lions were separated into four age-classes: foetus (6 months), pups (1 year), juveniles (1–3 years), and adults (4+). The foetal stage existed only to bring the foetus from weight 0 to 21 kg, their average weight at birth, and was 2 months shorter than the actual gestation period, given the von Bertalanffy growth curve parameters: $K = 0.282$ year^{-1} and maximum weight = 569 kg (Winship et al. 2001). Inclusion of the foetal life stage in the model was necessary to compensate for the growth calculation in Ecosim that uses a default value of –0.1 for the von Bertalanffy growth curve parameter t_0. When it comes to fish, t_0 is negligible given their weight at birth, whereas the bias becomes very important with mammals. The foetal stanza had no impact in the ecosystem model because foetuses incur a small mortality and feed on imported energy (i.e., via their mothers). Pups were differentiated from juveniles because they consume little if any prey and depend on their mother's milk for their first year of life (Trites et al. 2006*b*). Thus they also eat imports in the model. Although pups probably constitute easy prey for a large part of the year, their mortality is not dependent on the search for food, so the feeding adjustment of pups and embryo was set to zero in Ecosim. The ratio $W_{\mathrm{mat}}/W_{\infty}$ used in Ecopath to increase fecundity as body weight increases is unnecessary for mammals and was set to a very small value instead of zero (C. Walters, The University of British Columbia, Fisheries Centre, 2202 Main Mall Vancouver, BC V6T 1Z4, Canada, personal communication). In the Aleutians, annual instantaneous mortality rates (M) were 0.17 for adults, 0.24 for juveniles, and 0.52 for pups. These values were calculated from the slope of the natural log of numbers at age, based on published life tables (Trites and Larkin 1992). In SE Alaska, recent estimates from mark–resighting data in SE Alaska yielded lower rates of total annual mortality, averaging 0.11 for adults, 0.19 for juveniles, and 0.59 for pups (Pendleton et al. 2004).

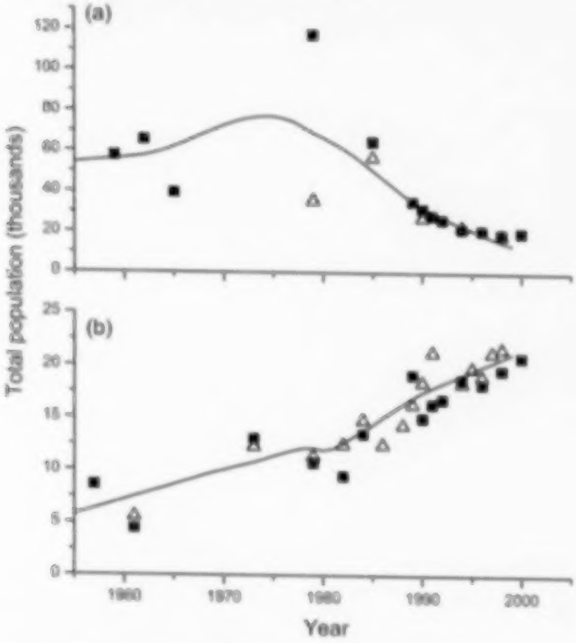
Table 2. Examples of modifications of diets from the 1990s to the 1960s for the Aleutian Islands and Southeast Alaska models.

	Aleutians								Southeast Alaska							
	Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder		Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder	
Prey	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1960s	1990s	1963	1990s	1963
Transient killer whales																
Toothed whales																
Baleen whales	1	1							4	6						
Steller sea lion																
Pup	1	10							1	0.4						
Juvenile	9	40							7	2.5						
Adult	6	30							35	13						
Small mammals	78	15							50	75.1						
Sea otter	4	3														
Birds	1	1							1	1	0.15	0.15				
Mammal-eating sharks																
Sharks and skates			0.7	0.7							0.5	0.5				
Salmon			10.6	10.6							14.21	20.21	1.79	1.79		
Pelagic, large											0.1	0.1				
Pelagic, small				2.7	0.098	0.1	3.8	3.8			5	5	5.01	5.01	12.63	12.63
Atka mackerel			41.6	42.7	15.7	15.7	19.6	19.6								
Sand lance			0.5	0.5	2.3	2.3					10.38	15	5.01	7.51	12.63	13
Pacific herring							0.2	0.2			26	15	7.28	2	15	3
Walleye pollock																
Juvenile			0.7	0.7	0.3	0.3	9.6	9.6			0.5	0.5			0.02	0.02
Adult			1	2.6	8.9	8.9	1.4	1.4			5.7	4	1.1	0.3	0.06	0.1
Pacific ocean perch			0.02								0.3	2	0.4	4	0.1	10
Rockfish, slope			1.5	1.6							2.63	5	2	2	1.1	1.1
Rockfish, shelf											1	3	0.8	0.8	0.2	0.2
Sablefish			0.1		1.7	1.7	1.1	1.1			0.2	0.2	0.3	0.3		
Pacific cod			6.3	6.3	0.7	0.7	0.2	0.2			0.9	4.13	1.4	2.4		
Pacific halibut			0.2								0.13	0.13				
Arrowtooth flounder			1.1	1							6.67	6.37	9.5	2.5		
Demersal, large			4.4	4.7	1.9	1.9	3.2	3.2			1.59	1.59	1.2	1.2	0.63	0.63
Flatfish			2.7	2.7	0.4	0.4					1.21	2.21	7.4	9.8	2.5	2.5
Demersal, small			16.2	16.2	4.8	4.8	4	4			16.42	8.5	8.79	12.37	26.14	27.2
Deepwater, large					1.9	1.9	3.2	3.2				0.04	0.04		0.5	1
Deepwater, small			1.6	1.6	2.6	2.6	25.8	25.8			0.84	0.84			14.8	14.92
Shrimps					1.9	1.9	18	18					1.22	1.22	6.09	6.09
Benthic invertebrates					1.8	1.8	3.7	3.7			0.63	0.63	5	5		
Epibenthic, carnivorous					17.7	17.7							36.83	36.83		
Cephalopods			8.1	8.1	32.4	32.4	0.5	0.5			4.9	4.9	2.91	2.91	3.04	3.04
Zooplankton, large							5.3	5.3					0.22	0.22	4.57	4.57
Zooplankton, small																

Table 2 (*concluded*).

	Aleutians								Southeast Alaska							
	Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder		Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder	
Prey	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1960s	1990s	1963	1990s	1963
Phytoplankton																
Marine plants																
Detritus					5.1	5.1	0.6	0.6					1.84	1.84		
Imports									2	2						

Fig. 2. Total population estimates obtained from Steller sea lion (*Eumetopias jubatus*) pups (open triangles) and non-pups (solid squares) and the estimated total population size (trend) obtained from a local regression model (Trites and Larkin 1996) for (*a*) the Aleutian Islands and (*b*) Southeast Alaska.



Steller sea lions abundance time series were obtained from a local regression model applied to counts of pups and non-pups made since 1956 (Trites and Larkin 1996). Sea lions were not counted continually over our study period (1963–2000). For example, counts in SE Alaska were only made once between 1961 and 1978, after which they were performed more regularly (Fig. 2). In the Aleutians, a number of rookeries were not counted during infrequent surveys, resulting in several years between 1963 and 1985 when counts were considered too partial to be included in the analysis. Thus in both areas, there was greater uncertainty in the population trajectory before the mid-1970s. Nevertheless, the results from these regressions represent the best estimate of abundance available. The proportion of juveniles and adults were calculated from a simple, age-structured population model and used as time series, while counts were used for pups. In the Aleutian Islands, the population totalled an estimated 57 653 animals in 1963, increasing to 72 113 in 1979, and declining to 13 852 in 2000 (Fig. 2). In SE Alaska, the number of sea lions increased from 8030 in 1963 to 21 175 animals in 1999.

Estimated number of Steller sea lions killed for subsistence, incidental harvest, shooting, and other sources of mortality were compiled from Wolfe et al. (2002), Perez (2003), Alverson (1992), and Trites and Larkin (1992) for the Aleutians. The hunting mortality for this area is rather small compared with that of the central GOA (see National Research Council 2003). No hunting was reported in SE Alaska.

Diets of Steller sea lions were estimated from the frequency of occurrence of prey remains found in scat samples in SE Alaska in the 1990s (A.W. Trites, unpublished data) and were modified to account for lower relative biomass of Pacific herring, salmon, and walleye pollock present in the ecosystem in the early 1960s. Thus, sea lion diet was dominated by salmon (~21%), sand lance (~15%), Pacific herring (~15%), arrowtooth flounder (~7%), and small demersal fish (~10%). Diet compositions obtained from similar studies for sea lions in the Aleutians (Sinclair and Zeppelin 2002) were dominated by Atka mackerel (33% and 40% for juveniles and adults, respectively), salmon (~11%), and small demersal fish (25% and 16% for juveniles and adults, respectively).

Although killer whales were the main predator of Steller sea lions in both models, Pacific sleeper sharks (*Somniosus pacificus*) could also contribute to sea lion pup mortality, as sharks are known to prey on mammals in Greenland (Hulbert et al. 2002). In Alaska, although marine mammals (mainly cetaceans) have been found with a frequency of occurrence of 15% in shark stomachs, it is not certain at this stage if they were eaten alive or scavenged (Hulbert et al. 2003). Loughlin and York (2000) assumed that sleeper and salmon (*Lamna ditropis*) sharks accounted for 1% of predation of sea lions when they tried to account for all sources of sea lion mortality. In the Aleutians, sharks were assumed to obtain 0.2% of their diet from pups and 3.5% from juvenile sea lions. In the SE Alaska model, sea lion pups and juveniles only supplied 0.1% of the shark diet.

Atka mackerel

Atka mackerel occur along the Aleutian chain but are most abundant at the western end (Scheffer 1959) and are practically nonexistent in SE Alaska. Stock assessment for this species only began in 1977, while the fishery started in 1972, with 4907 t being caught by the former USSR (Forrester et al. 1983). The biomass of Atka mackerel was estimated at 6.2 $t{\cdot}km^{-2}$ in 1979. In the absence of data, the 1963 biomass was estimated at 13.6 $t{\cdot}km^{-2}$ by Ecopath. Natural and fishing mortalities were estimated at 0.34 $year^{-1}$ and 0, respectively, in 1963. Maximum F was 0.17 $year^{-1}$ in 1996.

Pacific herring

Pacific herring does not seem to be prevalent in the western and central Aleutian Islands, but was abundant in the 1930s in the eastern Aleutians around Unalaska and Dutch Harbour (Scheffer 1959). In addition, most of the herring food and bait fishery in the Aleutian Islands are part of the fishery on the Eastern Bering Sea herring stock (Duesterloh and Burkey 2003). There were no estimates for herring biomass in this area.

In SE Alaska, Pacific herring has been exploited since the 1880s and was heavily exploited between the 1920s and the late 1960s (Hebert and Pritchett 2003). Fishing was reduced in the 1970s and the population increased rapidly afterward. The spawning biomass (3+) of the five main spawning areas was obtained from age-structured models (methods described in Carlile et al. 1996) and the more recent population estimates provided for 1977–2002 (D. Carlile, ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). The biomass trajectory for 1963–1976 was estimated using a stock reduction model (eq. 2) based on the 1977–2002 biomass and the 1900–2002 catch time series. The Schaefer biomass model was solved for k (assumed to be equal to biomass in year 1900) using a series of initial values of r because the data were not informative enough to estimate both parameters at once. The penalized likelihood was calculated using F prior calculated as $(F_{avg} - 0.07)^2$, where F_{avg} is the average fishing mortality (i.e., ratio of observed catches to the predicted biomass) for the years 1990–2001 (S. Martell, The University of British Columbia, Fisheries Centre, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada, personal communication). For a set of r values ranging from 0.3 to 0.7, the reconstruction model yielded a 1963 population biomass of 48 787 – 24 007 t as the likelihood increased. Based on the maximum acceptable value of annual fishing mortality rate fixed at 0.9 and the comparison of predicted 1977–2003 biomass trajectory with that calculated by the age-structured model, the initial intrinsic growth rate of 0.5 $year^{-1}$ yielded a reasonable estimate of 32 000 t (0.89 $t{\cdot}km^{-2}$) in 1963.

Salmon

Five species of salmon are present in the GOA, each spending various amount of time in fresh water, coastal areas, and offshore in the North Pacific. Except for some populations of Chinook (*Oncorhynchus tshawytscha*) in SE Alaska, coastal waters are part of the migrating route, as smolts migrate towards the GOA and return as spawners towards fresh water, one or more years later. Given the geographical boundaries of the ecosystem models, it was not possible to account for the whole life history of salmon, so they were regrouped and only spawners were considered in the model. As a consequence, salmon ecotrophic efficiency in the model was expected to be low.

The salmon present in the Aleutian Islands area are mostly part of the western Alaska stock, of the Bering Sea from the Yukon River to Unimak Island (Rogers 1987). These stocks migrate through the Aleutians from the Bering Sea to the GOA as smolts and back into the Bering Sea as adults (Scheffer 1959). Salmon catches from 1911 to 1997 were reported by Byerly et al. (1999), and no salmon catches were made since 1994 in the western Aleutians. As no biomass estimate was available, we used the catch in the entire Aleutian Islands as a proxy for salmon biomass trends, assuming that catches are proportional to biomass. The annual P/B for 1963 (1.17) was estimated based on the natural mortalities of the various salmon stocks (see Heymans 2005).

In SE Alaska, salmon spend only a small period of their life in coastal marine waters of the study area, where they sustain a large fishery. The catches in number and the average body weight of the catches by species for years 1969–2002 were provided by M. Kallenberger (ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). The natural mortality was taken from various sources (see Guénette 2005) and averaged at 1.44 $year^{-1}$. The fishing mortality time series was taken from stock assessments references for Chinook and coho (*Oncorhynchus kisutch*). For species more difficult to assess such as pink (*Oncorhynchus gorbuscha*), sockeye (*Oncorhynchus nerka*), and chum (*Oncorhynchus keta*), fishing mortality was based on recent estimates for each species, qualitative estimates of how the fishery evolved since 1963, and the catch times series (see Guénette 2005). Thus, fishing mortality in 1963 was assumed to be the same as it was in 1977 (0.67 $year^{-1}$), and the biomass was estimated at

1.11 t·km^{-2}. Although the biomass time series data are not very good, since we had to interpolate for several years for pink, chum, and sockeye, they conformed with the increase in abundance observed for several species (especially pink salmon, the most abundant species) in catch and abundance index since the 1970s (H. Geiger, ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). To balance the model, salmon diet had to be modified to increase the imports from 75% to 93%, implying that a larger part of their life history and feeding behaviour takes place outside the study area.

Pacific halibut

The Pacific halibut survey estimates for the western Aleutians were obtained from Ronholt et al. (1994) for 1980–1986 and from Zenger (2002) for 1991–2002, giving estimates of 0.29 t·km^{-2} for 1979 and 0.58 t·km^{-2} for 1991. No estimates of biomass were available for 1963. P/B (0.19 year^{-1}) was based on a natural mortality estimated at 0.1 year^{-1} (Pauly's empirical equation) and fishing mortality equal to that of 1991. Catches were taken from Forrester et al. (1978) for 1963–1970, from Forrester et al. (1983) for 1971–1973, from Clark and Hare (2003) for 1974–1980, and from the International Pacific Halibut Commission (IPHC) web site (http://www.iphc.washington.edu/halcom) for recent years. In absence of reliable estimates of F, halibut catches were forced in the model.

In SE Alaska, Pacific halibut biomass, effort, and fishing mortality (1974–2001) were all taken from assessment reports (Clark and Hare 2002) for IPHC Area 2C, which covers the area delimited by 137°W. Catch statistics for 1929–2002 were available from the IPHC web site. The biomass of legal size (larger than 80 cm, which corresponds to age 4–5 in the 1990s) was estimated at 0.64 t·km^{-2} in 1999, and the biomass of small individuals was considered negligible. In 1977, the biomass amounted to 18 794 t or 0.26 t·km^{-2}. Natural mortality was estimated at 0.1 year^{-1} (Pauly's empirical equation), and fishing mortality was estimated at 0.16 year^{-1} and 0.1 year^{-1} in 1999 and 1977, respectively. In 1963, the catches amounted to 6192 t, and the biomass was assumed to be similar to that of 1974, which seemed to be sufficient to balance the model and fit the time series.

Arrowtooth flounder

The biomass of arrowtooth flounder in the Bering Sea – Aleutian Islands was estimated at 284 965 t (0.52 t·km^{-2}) in 1979 (Wilderbuer and Sample 2003). No biomass estimate was available for 1963. Catches for 1970–2002 were taken from the stock assessment report, which peaked around 6500 t in 1979 and again around 5000 t in 1991 (Wilderbuer and Sample 2003). After 1997, catches decreased because of fisheries restrictions and the phasing out of the foreign fishery. Arrowtooth flounder has a low commercial value and are mostly discarded in various trawl and longline target fisheries, with the largest discards being in the Pacific cod (*Gadus macrocephalus*) and flatfish fisheries (Wilderbuer and Sample 2003). Prior to 1970, catches of all flounders combined were given by Ronholt et al. (1994), which we prorated by the ratio of arrowtooth flounder to other flounder given by Anonymous (2001). In 1963, the natural mortality rate of 0.3 year^{-1} (Wilderbuer and Sample 2003) was used as an estimate of P/B, assuming that fishing mortality was negligible. The average annual Q/B (2.6) ratio for adult arrowtooth flounder was obtained from NFMS data.

In SE Alaska, biomass was calculated using the stock assessment for the whole Gulf, assuming that SE Alaska contained 13% of the GOA biomass (J. Turnock, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration (NOAA), 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA, personal communication) and that the same percentage was valid for the whole time series. Catches for the period 1991–2002 were taken from the NOAA database. Before that, arrowtooth flounder were mostly discarded and declared as part of the flatfish group. In the NMFS database, all flatfish were reported together in 1956–1970 and 1977–1990, so we assumed that two-thirds of the flatfish were arrowtooth flounder (J. Berger, Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA, personal communication). Catches were generally under 1000 t annually, except in the 1970s when it approached 5000 t. Fishing mortality was estimated at 0.0006 year^{-1} in 1963. Natural mortality (0.2 year^{-1}) was taken from Turnock et al. (2002). A Q/B ratio of 1.05 year^{-1} was calculated using a P/Q of 0.2.

Fitting the model

Time series of biomass, catches, and fishing mortalities were used to fit the models for the period 1963–2002. The models were driven with fishing mortality and fitted by trying to obtain predicted biomass and catches trajectories similar to those observed during the study period for marine mammals as well as for fish. The model was first fitted manually to identify possible solutions and the most sensitive parameters, modifying initial biomass, biomass accumulation, and predation vulnerability (Table 1). This resulted in making some manual modifications to the biomass accumulation rates (see Table 1). Other corrections to biomass accumulations were necessary because of the history of some fisheries, but we did not undertake to include them and explore their impact until we began fitting the time series. For example, the only way to fit the Pacific herring time series data was to include a negative biomass accumulation that acknowledges that the herring population was not stable when we started the model in 1963. It was also necessary to increase the initial biomass of sablefish in the SE Alaska to obtain predicted catches as high as those observed. For the Aleutians model, Pacific halibut was attributed a positive biomass accumulation because of the increase in population abundance observed between 1963 and 2002.

However, this method of adjusting the model is unlikely to produce an optimal solution in a timely manner, and therefore we preferred formal fitting to the time series by using a nonlinear search procedure, allowing vulnerabilities to be modified. We used the knowledge gained in the manual fitting to start the search procedure with different initial parameters to avoid being caught in local optimal solutions. The criterion was a weighted sum of squares of deviations (SS) between logarithms of observed and predicted biomasses and catches. Climate influences (e.g., Pacific Decadal Oscillation (PDO)) on the ecosystem productivity were also included in the model to improve the fit to time series. Although the search for an optimal solution does not result

Table 3. Biomass and prey of transient killer whales in the Southeast Alaska and four scenarios used for the Aleutians models.

	Aleutians				
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Southeast Alaska
Biomass ($t\cdot km^{-2}$)	0.0003	0.0006	0.0006	0.0003	0.0007
Prey (%)					
Baleen whales	1	5	1	1	6
Steller sea lion					
Pup	1	8	10	10	0.4
Juvenile	9	12	40	40	5
Adult	6	8	30	30	13
Small mammals	78	62	15	15	72.6
Sea otter	4	4	3	3	0
Birds	1	1	1	1	1
Imports	0	0	0	0	2

in a unique solution given that the data is generally imperfect, one should not presume that just any parameter modification would result in a good fit. The food web interactions and the numerous time series constitute strong constraints that reduce the range of possible solutions.

Recent work using Ecosim without time series data has been useful on theoretical grounds to explore the effect of model structure and complexity on the simulated responses to disturbances (e.g., Vasconcellos et al. 1997; Fulton et al. 2004; Pinnegar et al. 2005) and the impact of alternative trophic functional relationships on model behaviour (Mackinson et al. 2003). This modelling approach does not mean that all combinations of parameter values are equally possible and falls short when evaluating and comparing scenarios without the benefits of having time series data. It is particularly difficult to differentiate between high growth rate – low initial biomass and low growth rate – high initial biomass scenarios without time series data. Thus, the Ecosim approach that uses time series data is far superior to comparing characteristics of Ecopath models in spite of any apparent inaccuracies that this modelling method may have. For example, using models for recent years for which there is obviously more available data would not allow the role of change in ocean productivity to be evaluated nor to understand what happened during the 1970s.

The PDO was used to modify the productivity of primary producers and account for changes in oceanic regimes in the Pacific Ocean (Hare and Mantua 2000). Monthly values of PDO (http://jisao.washington.edu/pdo/PDO.latest) were transformed to obtain a range of 1 and were used directly in SE Alaska, which improved the fit to the time series. In the Aleutians, it was necessary to use the inverse PDO (Heymans et al. 2005). This is consistent with the fact that the PDO is inversely related to sea surface temperature in the Aleutians and positively correlated in SE Alaska (Mantua et al. 1997). Similarly, during positive PDO years (1977 and onwards), annual discharge in the Skeena River, at the southern limit of SE Alaska, averaged 8% lower than that in the negative PDO years (before 1977) (Mantua et al. 1997). In contrast, discharge in the Kenai River in the central GOA in positive PDO years averaged 18% higher than that during the negative years.

Simulations

Given the uncertainty about killer whale parameters, we evaluated the impact of the initial killer whale abundance and their diet by comparing the results of four scenarios using the Aleutian Islands model. Scenario 1 started with a low biomass of killer whales (0.0003 $t\cdot km^{-2}$) and assumed that Steller sea lions constituted only 16% of the killer whale diet (Table 3). The second scenario used a higher estimate of killer whale biomass (0.0006 $t\cdot km^{-2}$) and assumed that sea lions provided 28% of killer whale nutritional needs. At high killer whale biomass, small mammals were not abundant enough to provide 78% of killer whales needs, which were therefore reduced to 62% (Table 3). Scenario 3 also used the higher estimate of killer whale biomass and assumed that sea lions were the main prey for killer whales, for a total of 80%. Scenario 4 featured a low killer whale biomass, with sea lions being a preferred prey for killer whales, constituting 80% of their dietary needs.

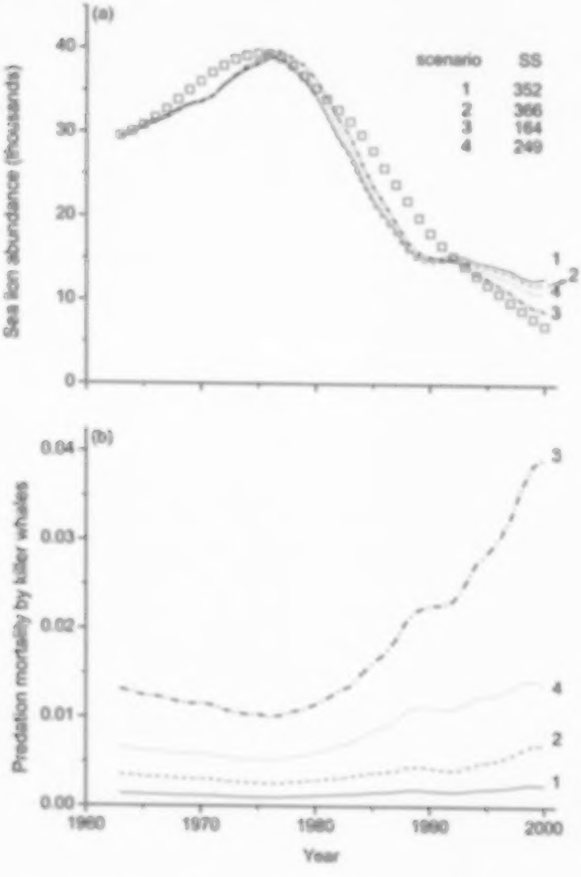
The predicted trajectory of Steller sea lions was likely due to a combination of several factors. After identifying the most likely sources of influence on the sea lion abundance trajectory, we examined their respective influence by removing them one at a time. Simulation results for each scenario were compared based on the shape of sea lion abundance trajectories and the sum of squares between the observed and predicted times series of adult sea lion abundance. For convenience, the sums of squares were divided by 10^6. We chose to compare scenarios showing total adult sea lion abundance trajectories given that the abundances of the three modelled stanzas were correlated.

Results

Aleutian Islands

Ecosim predicted an initial increase in the Steller sea lion population in the Aleutians followed by a steep decline after 1975, which yielded a good fit to the reference time series

Fig. 3. (*a*) Trajectory of adult Steller sea lion (*Eumetopias jubatus*) abundance in the Aleutians under four scenarios: (1) low abundance of killer whales (*Orcinus orca*) and low predation on sea lions; (2) high abundance of killer whales and low predation on sea lions; (3) high killer whale abundance and high predation on sea lions; (4) low killer whale abundance and high predation on sea lions. The sums of squares (SS) for each scenario are provided. The reference abundance data is represented by squares. (*b*) Annual instantaneous predation mortality rate on adult sea lions under each scenario.



for all scenarios of killer whale abundance and diet allocations (Fig. 3*a*). The main difference between scenarios was the steepness of the sea lion decline in the 1990s. As killer whale predation on sea lions increased, the rate of decline in sea lions increased under all scenarios (Fig. 3*a*), regardless of how killer whale predation was distributed among age classes or stanzas (pups, juveniles, adults). The steep decline in the 1990s suggested by the reference data was more closely matched by scenario 3, which assumed a high killer whale biomass and a high proportion of sea lions in killer whale diet. The initial proportion of sea lion in the diet of killer whale had a dramatic effect on the instantaneous rate of mortality inflicted on sea lions. Under scenario 3, annual mortality of pups caused by killer whales increased from 0.32 in 1963 to 0.98 in 2002 (Fig. 3*b*). In comparison, when a low rate of predation was inflicted by killer whales in scenario 1, the annual mortality remained about constant (0.03) throughout the study period. Adult sea lion mortality caused by killer whale predation, although smaller, followed the same trends. Note that in contrast with killer whale-induced mortality, the mortality caused by hunting and incidentals from conflict with fishing reached a maximum of 0.01 year^{-1} in the 1980s for juvenile and adult sea lions.

The third scenario provided the best fit to the data and was therefore used as the baseline for further simulations. Model predictions from Ecosim corresponded fairly well with the abundance and catch data of commercial fish, sea lions, and other mammals (Fig. 4). Ecosim predicted that both small mammals and sea otters would have declined starting in the mid-1970s. However, predictions for small mammals are difficult to evaluate given the paucity of the data and a general lack of information. In the case of sea otters, the observed decline in recent years was not completely explained by the model, the slope of the decline not being steep enough to mimic the observed sea otter depletion.

Ecosim predictions for Atka mackerel matched the stock assessment trends, except for the 1970s and late 1990s. In addition, Ecosim predicted that the 1960s biomass would be similar to that of 1992 (~13 t·km^{-2}). It should be mentioned here that the parameters used to fit Atka mackerel had a direct impact on the trajectory of sea lions after 1977. By assuming a vulnerability of about 2 for Atka mackerel, the declining slope shifted to the left starting in the 1980s, suggesting an earlier decline of sea lions, while a lower vulnerability (<1.5) resulted in a sea lion decline occurring closer to the reference data (Fig. 4). The lower vulnerability indicates that sea lions were eating Atka mackerel at close to the maximum rate limited by mackerel behaviour.

The 1963 walleye pollock biomass was estimated at ~6–8 t·km^{-2}, which was similar to that of the 1990s. According to data, Pacific halibut increased by about threefold between 1980 and 2002, and this was well reproduced by the model predictions. In addition, the model predicted a Pacific halibut biomass of 0.4 t·km^{-2} in 1963 or twice as much as that of 1980 (0.17 t·km^{-2}). The trends observed for the Pacific ocean perch were mainly dominated by the large overexploitation of the 1960s. However, it was impossible to recreate the high level of catches of the 1990s suggested by the data (Fig. 4). The trends for arrowtooth flounder, Pacific cod, and sablefish were only vaguely similar to the time series. As expected, Ecosim could not capture the dynamics of salmon because most aspects of the species' life histories occur outside of the study area. In the Aleutians, however, salmon is only a minor player (in the sense of being a minor prey for sea lions) and did not have much impact on the model outcome.

The simulations indicate that fishing, environmental variations, killer whale predation, and competition with Pacific halibut were all important factors in determining the Steller sea lion population trajectory. We therefore examined each of these factors individually in terms of their direct effect on sea lion numbers using the SS between the baseline sea lion trajectory and the abundance time series as a measure of fit. The SS of the best-fitting model (using all factors) was 164. Ecosim captured the increase of sea lion abundance that

Fig. 4. Comparison of the reference (*a*) biomass ($t \cdot km^{-2}$) and (*b*) catch ($t \cdot km^{-2} \cdot year^{-1}$) times series data (squares) and Ecosim predictions (lines) for 12 functional groups in the Aleutians model. The dotted lines show the effect that increasing the vulnerability of Atka mackerel (*Pleurogrammus monopterygius*) has on trajectories of Atka mackerel and Steller sea lions (*Eumetopias jubatus*). The thin line for sea otters (*Enhydra lutris*) in panel *a* shows the trajectory abundance in the absence of killer whales (*Orcinus orca*). Triangles indicate forced catches.

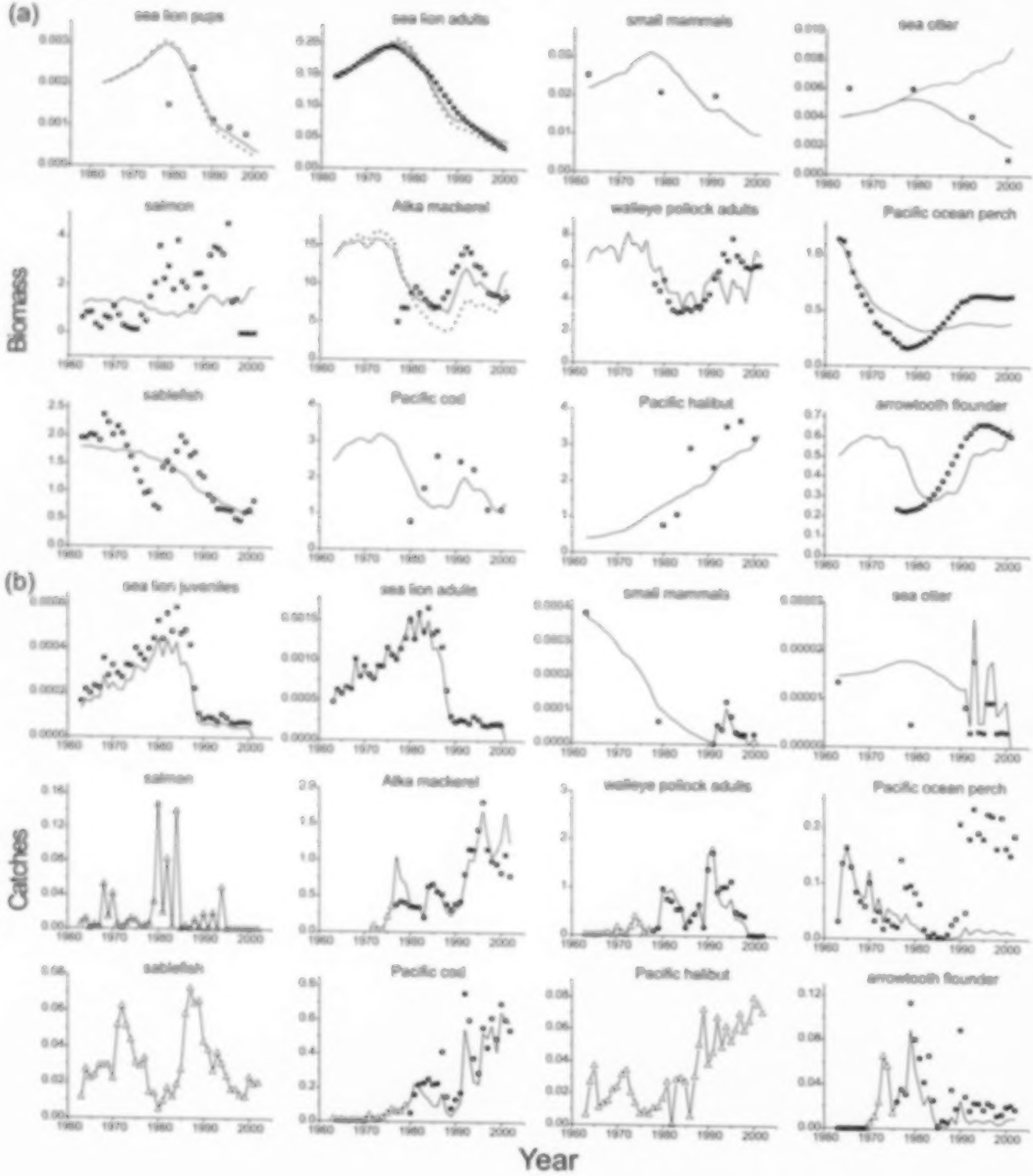
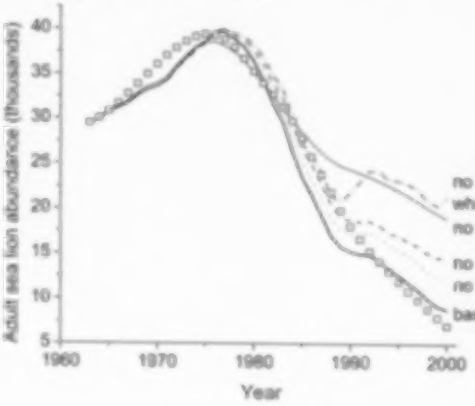


Fig. 5. Relative impact of removing (*i*) Pacific halibut (*Hippoglossus stenolepis*) and (*ii*) killer whales (*Orcinus orca*), (*iii*) banning fishing, and (*iv*) removing the Pacific Decadal Oscillation (PDO) from the model, starting in 1975. The reference time series is represented by squares, and the sums of squares (SS) are given for each scenario.



occurred in the 1960s because of the influence of the PDO, but when the effect of the PDO was removed starting in 1975, the model predicted that sea lions would have only declined by a small number from 1975 to 1998 (Fig. 5). The resulting SS was 1150.

Depleting killer whales starting in 1975 showed that Steller sea lion numbers would have still declined but that the decline would have been less extreme (SS = 1338). The model indicates that sea lions would have declined until 1989, then increased abruptly between 1989 and 1992, followed by a soft decline thereafter. The abrupt change in 1989 is linked to the increase of Atka mackerel biomass during this period (Figs. 4 and 5). In the absence of killer whales, the model predicted that sea lions would become more abundant and would have inflicted more predation mortality on Atka mackerel. This is turn would have caused sea lions to increase the time they spent feeding, as well as exposed them to higher predation risks.

A simulated ban on fishing starting in 1975 lessened the Steller sea lion decline compared with the baseline (Fig. 5). However, the impact was not as important as that of the other scenarios, increasing the SS to only 338. Atka mackerel, being the preferred prey and the principal fishing target, explained 63% of the effect of banning fishing.

In the absence of Pacific halibut, for which we simulated a depletion starting in 1975, Steller sea lions maintained a higher level of abundance than the best fit trajectory, for a total SS of 205 (Fig. 5). The impact from Pacific halibut depletion was the least important of the four factors considered. The competition between sea lions and halibut was mainly due to their common prey, Atka mackerel. As the predicted halibut biomass increased ninefold between 1963 and 2000 (Fig. 4), the predation mortality inflicted by halibut on Atka mackerel was predicted to rise from 0.005 to 0.04 year^{-1}.

It is noteworthy that the factors examined above have the same relative effect on the ecosystem overall as they do on Steller sea lions alone. Thus, the strongest effect on most observed groups was climate, while the absence of killer whales had the second most important effect, followed by fishing and Pacific halibut competition. It is interesting that the model predicts an increase in the abundance of sea otters in the absence of killer whales (Fig. 4).

Southeast Alaska

For the SE Alaska model, Ecosim predicted that Steller sea lion abundance would generally increase between 1963 and 2002 (Fig. 6). However, Ecosim predicted that the abundance of sea lions decreased in the 1960s–1970s, reaching lower levels than what the reference time series suggested. In addition, it was impossible to emulate the continuous increase of the 1990s. The reasons for these discrepancies will be explored below.

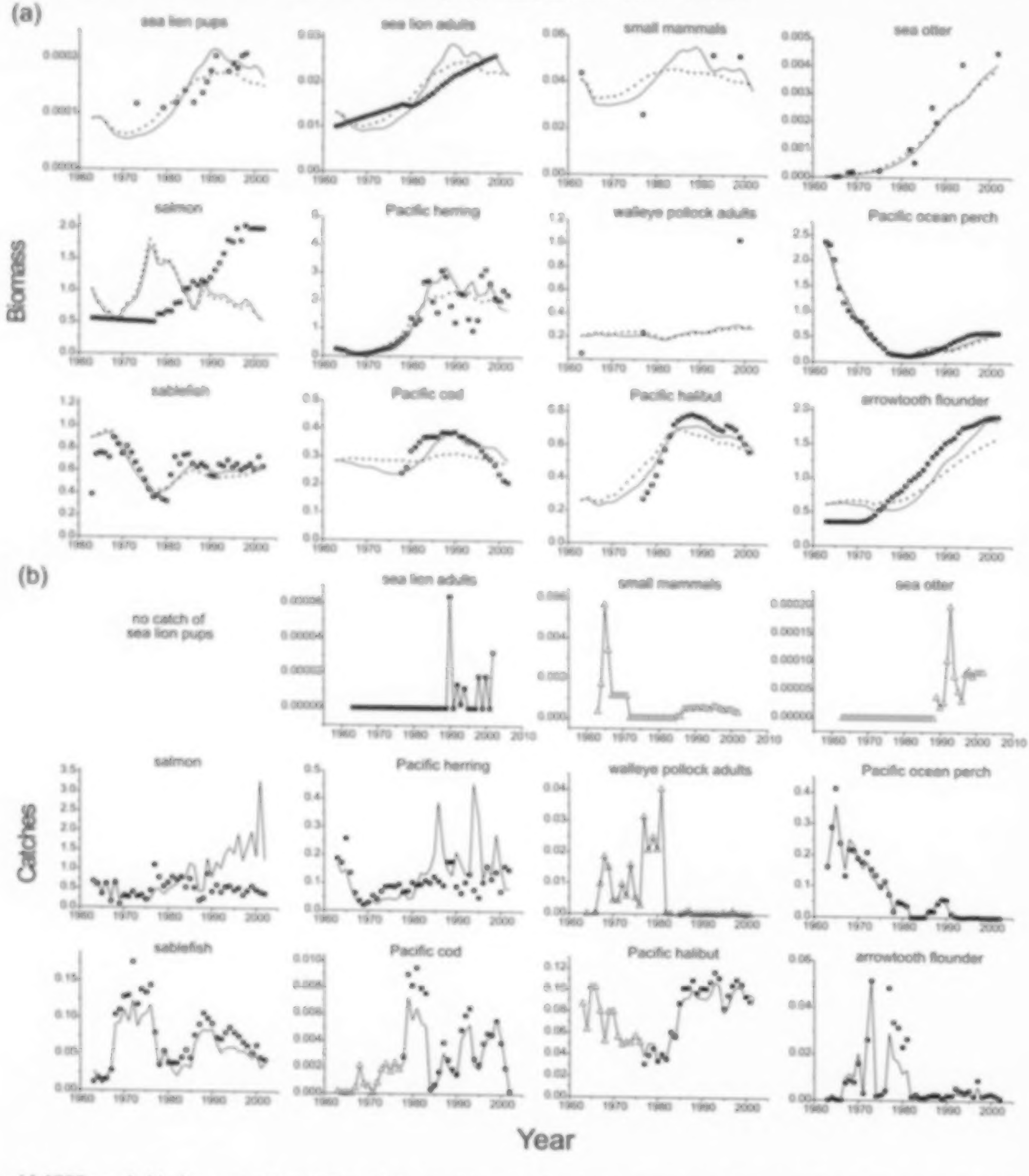
As for the preceding model, the SE Alaska model failed to capture the dynamics of salmon because most aspects of the species life histories occur outside of the study areas. However, Ecosim predictions were quite close to the observed biomass for Pacific herring, Pacific ocean perch, sablefish, Pacific cod, and arrowtooth flounder (Fig. 6). Pacific herring was predicted to increase at the end of the 1970s and stayed high in the following years. However, the highly variable herring recruitment was not captured by Ecosim. Annual mortality caused by killer whale predation on sea lion pups reached 0.34 in 1963, a value similar to that of the Aleutians. However, contrary to the Aleutians model, mortality decreased through time (to 0.26 year^{-1} in 2002) as sea lion biomass increased. Sea otters only increased if the vulnerability parameter of otter prey was increased. Unfortunately, the data available and included in the model offered no further insights into sea otter dynamics (Guénette 2005).

Simulations showed that Pacific herring and salmon biomass, environmental variations, competition with arrowtooth flounder, and killer whale predation were factors that could impact the Steller sea lion abundance trends. The SS between the baseline scenario and the reference time series reached 112. When ignoring the PDO, the biomass trajectory of Pacific halibut, Pacific cod, and especially Pacific herring was flattened considerably (Fig. 7*a*). The impact of the PDO was more obvious on Pacific herring for which the increase of the late 1970s was lessened to half of the observed peak biomass. As a consequence, Ecosim predicted that the sea lion trajectory would be flattened (Fig. 7*a*), decreasing less in the 1970s, and reaching lower levels in the 1990s; thus the SS increased to 119.

A simulated depletion of killer whales starting in 1963 resulted in a steady increase in Steller sea lion abundance for the whole study period and yielded the highest SS (203). Depleting arrowtooth flounder caused sea lion abundance to increase more steeply in the 1980s, but still caused sea lion numbers to flatten out in the 1990s. Under this scenario, the SS decreased to 77. It is worth noting that Pacific herring predation mortality caused by arrowtooth flounder increased over time (threefold) as arrowtooth flounder abundance increased (sevenfold). Depleting Pacific halibut did not have any substantial effect on sea lion abundance.

Simulating a ban on Pacific herring fishing starting in 1963 resulted in Steller sea lions increasing steadily and reaching a higher level of abundance than the baseline by the late 1960s. Sea lion numbers started to decline in the

Fig. 6. Comparison of the reference (*a*) biomass (t·km^{-2}) and (*b*) catch (t·km^{-2}·year^{-1}) time series data (squares) and Ecosim predictions (lines) for 12 functional groups in the Southeast Alaska model. The dotted lines show the impact of ignoring the Pacific Decadal Oscillation in the Ecosim simulations for each functional group. Triangles indicate forced catches.



mid-1980s probably because of the failure of the model to account for increases in salmon (Fig. 7*a*). This scenario increased the SS to 129. Forcing the salmon biomass to match the times series, however imprecise it was, caused sea lion abundance to continue increasing during the 1990s, following the data trend quite closely and reducing the SS to 72 (Fig. 7*a*).

Based on the many studies that have either used Ecopath alone or have used Ecopath with Ecosim without time series

Fig. 7. (*a*) Relative impact of removing (*i*) killer whales (*Orcinus orca*) and (*ii*) arrowtooth flounder (*Atheresthes stomias*), (*iii*) banning Pacific herring (*Clupea pallasii*) fishing (no F herring), (*iv*) removing the Pacific Decadal Oscillation (PDO), and (*v*) forcing salmon biomass in the Southeast Alaska model. (*b*) Relative impact of the same scenarios when the proportion of herring in the initial Steller sea lion (*Eumetopias jubatus*) diet was reduced. The sums of squares (SS) for each scenario are provided.

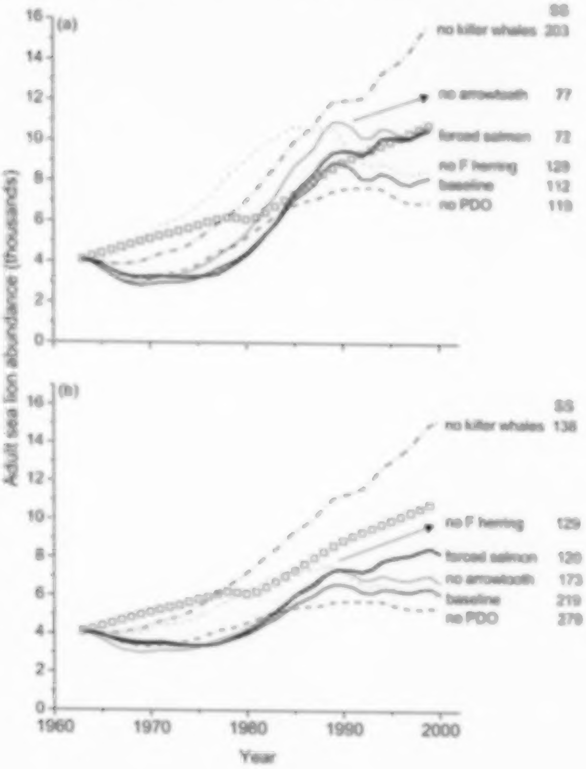
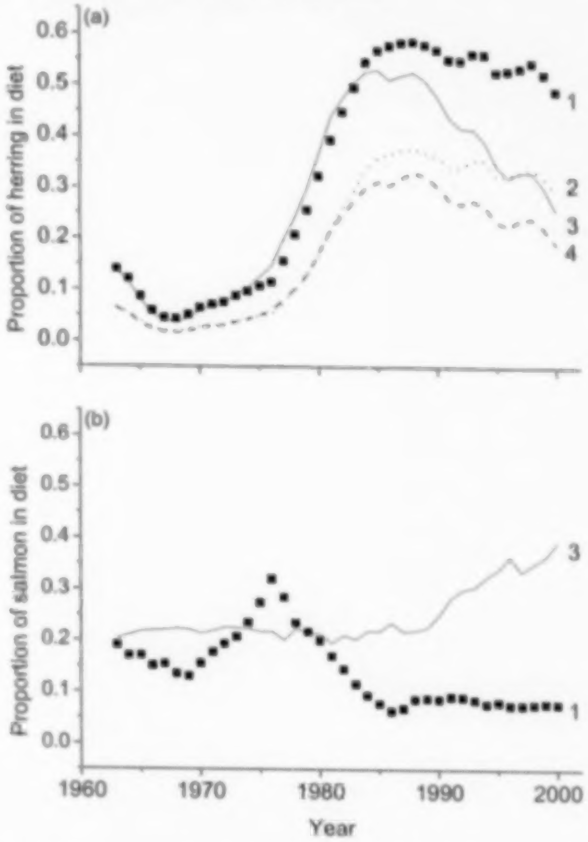


Fig. 8. Trajectories of the proportion of (*a*) Pacific herring (*Clupea pallasii*) and (*b*) salmon (*Oncorhynchus* spp.) in the Steller sea lion (*Eumetopias jubatus*) diet in the Southeast Alaska model under four scenarios: (1) original sea lion diet; (2) sea lion diet reduced in herring; (3) original diet and forced salmon; (4) reduced diet and forced salmon.

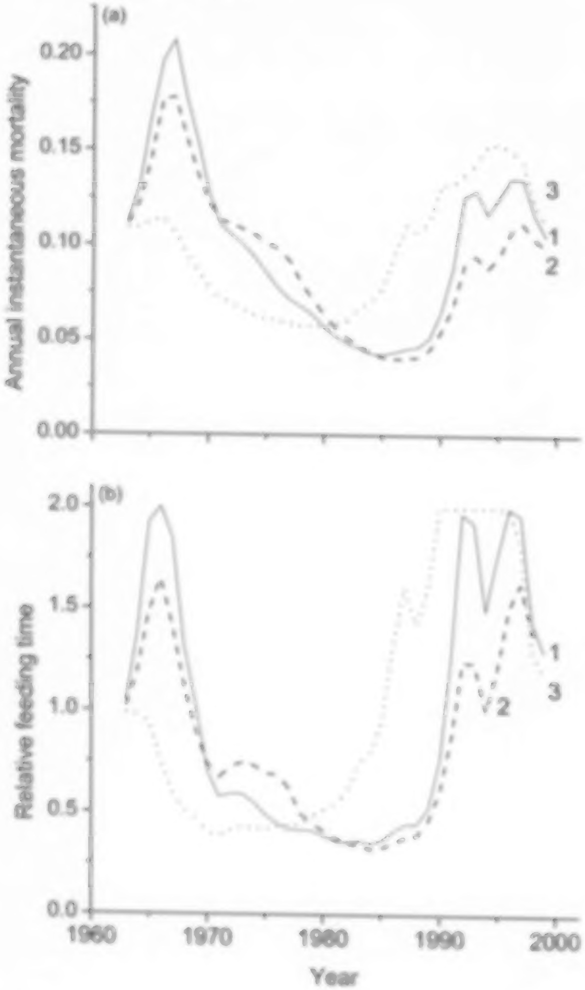


data, it is common to assume that the initial diet is crucial to the outcome of simulations. To verify this, we used Steller sea lion predation on Pacific herring in the GOA as an example of how the initial parameters have a limited influence on model outcomes. If the proportion of herring in the initial sea lion diet had been reduced to 7% instead of 15% of the working model, sea lions would not have increased as much (Fig. 7*b*). The trajectories of sea lion abundance resulting from each scenario tell a similar story about the relative importance and relative effect of each scenario, except that a change herring abundance would have a lesser impact on sea lion abundance if herring was initially less important in the sea lion diet, as demonstrated by the relative SS (Fig. 7*b*). When salmon biomass was not forced, the trajectories of proportion of herring in the sea lion diet followed similar general patterns over time because of the increase in herring in the ecosystem (Fig. 8*a*). The proportion of herring in the sea lion diet in 1999 reached 52% for the initial herring scenarios and 32% for the reduced herring scenarios. Forcing salmon biomass resulted in Ecosim predicting that the proportion of herring in sea lion diet would decline starting in the late 1980s, reaching 30% in the original diet scenario and 22% in the reduced diet scenario in 1999. Thus, the dynamics of predation on herring resulted in a proportion of herring in sea lion diet that is comparable with that used in the original diet used in the balanced 1999 model (26%). In comparison, when the salmon was forced, its biomass increased in the 1980s–1990s, and thus, the proportion of salmon in the sea lion diet would increase (Fig. 8*b*).

Predation on Steller sea lions results from a combination of killer whale abundance, killer whale diet preference, and the risk that sea lions take to find their prey. Sea lion mortality and feeding time increased in the 1990s as salmon biomass plummeted in the baseline model. Forcing salmon biomass to increase in the 1990s resulted in less sea lion mortality (Fig. 9*a*) as their feeding time decreased (Fig. 9*b*). Similarly, in absence of fishing for Pacific herring, sea lions' feeding time and total mortality decreased in the 1960s–1970s (Fig. 9).

The present model did not capture the increase in walleye pollock biomass (Fig. 6) suggested by admittedly very sparse data (Alton 1981; M. Sigler, National Marine Fisheries Service, Auke Bay Laboratory, 11305 Glacier Highway, Juneau,

Fig. 9. Southeast Alaska adult Steller sea lions (*Eumetopias jubatus*) total annual instantaneous mortality (*a*) and relative feeding time (*b*) for three scenarios: (1) baseline, (2) forced salmon (*Oncorhynchus* spp.) biomass, (3) no fishing for Pacific herring (*Clupea pallasii*).



AK 99801, USA, personal communication). However, recent studies show that walleye pollock is consistently present in feeding areas such as Benjamin Island (SE Alaska) and constitute a reliable prey for Steller sea lions, being found in 86% of scats (Womble and Sigler 2006). In contrast, larger scale studies in SE Alaska show frequency of occurrences of about 50% (Trites et al. 2007). Given the small initial walleye pollock biomass in the model, their contribution to sea lion diet is quite small (around 5%). We wanted to verify the impact of walleye pollock on sea lion trajectories when (*i*) the initial biomass and the biomass accumulation were higher and (*ii*) walleye pollock contribution to sea lion diet was increased to 12%. However, none of these scenarios caused a major changed in the sea lion trajectory.

Discussion

The choice of the model area delimitation corresponded to Steller sea lion population trends and perceived homogeneity of ecosystem features based on oceanography, fish composition, and geography. Our goal was to minimize the occurrence of contradictory sources of variation affecting the trend in sea lion abundance within a model area. We expected that a coastal model would be suited for sea lions as well as other coastal species. The downside of this approach is the lack of fit to the data for species that have a larger distribution area and depend less on the modelled area. For these species, the usual approach is to assume that the population of the modelled area is proportional to the biomass estimated by area, which in Alaska determines the level of catch allocated in each area. All of the population dynamics are then assumed to happen within the model area. This can be true and sufficient in some cases and can explain some discrepancies in other cases. The sablefish population is a good case at hand, as it is considered a single stock and yet shows substantial movement among the Bering Sea, the Aleutian Islands, and the GOA. Its preferred habitat is the eastern GOA, which may explain in part why the match to sablefish biomass time series data was better in SE Alaska than it was in the Aleutians model.

SE Alaska and the western Aleutian Islands are dynamic ecosystems influenced by a combination of factors that have to be considered simultaneously to explain the events of the past 40 years. In both case studies, the ecosystem models successfully reproduced the Steller sea lion abundance trends as well as those of other exploited groups of species. Admittedly, there is a lack of information for diets in the 1960s as well as abundance data for important species such as Atka mackerel, Pacific halibut, and walleye pollock. However, a number of our simulations confirmed that the initial dietary values were not as important as the rates of change of biomass through time. Simulations that used dramatically different initial biomass estimates of Atka mackerel showed that it is unlikely that the biomass trajectories between 1963 and 1980 could have differed much from our predictions and still yielded the reported fishing catches irrespectively of their importance to predator diets (S. Guénette, unpublished data). Data is admittedly missing on forage fish trends in this region and could modify the model behaviour if we could have included their dynamics. The biomass trajectory of walleye pollock in SE Alaska is largely unknown, although localized estimates suggest that walleye pollock abundance increased since the 1970s. Our simulations suggest that walleye pollock had a secondary role in determining sea lion abundance trajectories in both ecosystems during this study period. However, their role may change as walleye pollock and Pacific hake (*Merluccius productus*) increase in SE Alaska. Finally reducing the proportion of Pacific herring in the sea lion diet changed the absolute rate of increase of sea lions but did not appreciably change the relative importance of each of the important controlling factors in the SE Alaska model.

According to Ecosim predictions, change in ocean productivity and killer whale predation explain a large part of the Steller sea lion decline in the Aleutians, while fishing and competition with Pacific halibut also played a role. Fishing was important mainly through its impact on Atka mackerel. In SE Alaska, Ecosim predictions did not follow the sea lion data as closely as it did in the Aleutians model. Simulations suggested that Pacific herring and salmon biomass, killer whale predation, competition from arrowtooth flounder, and the 1976–1977 change in ocean productivity could explain the continuous increase in sea lions between 1963 and 2002. The increase in abundance of sea lions in SE Alaska in the 1970s–1980s paralleled the increases in herring and salmon. The discrepancy between observations and model predictions in the 1960s–1970s reflected the depletion of herring by fishing, killer whale predation, and the PDO, while in the 1990s, the model did not capture the increase of salmon.

Loughlin and York (2000) noted that Steller sea lions in both regions of Alaska experienced similar sources of mortality (i.e., killer whale predation, the influence of PDO on fish trajectories, and the influence of fishing). One exception was that subsistence hunting only occurred in the Aleutians. The index of ocean productivity (the PDO) had inverse effects in the two ecosystems studied and caused downward trajectories in several species of fish in the Aleutians in contrast with the upward trends in SE Alaska. However, ocean productivity impacted the Aleutians model more than the SE Alaska model. It is also clear that Pacific herring recruitment success was due to a combination of factors and was not the sole result of the PDO. This is to be expected in an environment where glaciers, bays, streams, and fjords have an influence. The models suggest that fishing played a structuring role in the dynamics of both ecosystems mainly through removing Atka mackerel in the Aleutians and herring in SE Alaska. Given the initial settings, sea lion mortality caused by killer whale predation in 1963 was equivalent in both models, but followed different trajectories. The impact of killer whale predation had the greatest impact when sea lion abundances were low (i.e., in the 1990s in the Aleutians and in the 1960s in SE Alaska).

The competition with large flatfish was one of the more interesting predictions of the simulations. Pacific halibut in the Aleutians and arrowtooth flounder in SE Alaska have increased dramatically in the last 40 years. The impact of these large flatfish is relatively small compared with the other factors, but their predatory effect on the most important prey species of their respective ecosystems makes them important over time. Halibut does not seem to play this role in SE Alaska probably because it did not increase as dramatically and it is only a minor competitor for Pacific herring. The competition with flatfish has also been pointed out in simulations with the Eastern Bering Sea models in two different contexts. Simulations from the 1980s Bering Sea model highlighted considerable overlap in diet of Steller sea lions and large flatfish and showed that their removal could increase the sea lion populations (Trites et al. 1999). Using a slightly different model for the Bering Sea, Aydin (2002) showed that increasing the fishery for flatfish and, depending on the initial assumptions, a decrease in the walleye pollock and Pacific cod fisheries could also result in an increase in sea lions.

The biomass of killer whales and their prey preferences are highly uncertain in both ecosystem models. In such models, the proportion of the diet made up by any one species depends on the initial diet used in the model and the changes in biomass that occur in the ecosystem. In the Aleutians, results showed that killer whale biomass and the proportion of Steller sea lions in their diet needed to be high in order for the observed 1990s decline in sea lions to have occurred. The model also assumed a strong predator–prey relationship existed between both species. However, other plausible scenarios of predation and behaviour cannot be discounted. For example, the same end results could have been obtained if several pods of killer whales had started to specialize in hunting sea lions in the 1980s (e.g., Matkin et al. 2002). For instance, the "Kodiak killers", a group of six killer whales that frequents the waters around Kodiak Islands (GOA), are believed to have specialized hunting on sea lions (NPUMMRC 2006). There are other indications that some killer whales may develop specialized hunting behaviour, such as attacking sea otters (Estes et al. 1998), gray whale calves (*Eschrichtius robustus*) (Matkin et al. 2006), or beluga whales (*Delphinapterus leucas*) (Shelden et al. 2003) in difficult to access areas in spite of dangers of getting stranded (Frost et al. 1992). The structure of our model does not account for pod-based changes in behaviour. However, there seems to have been little incentive for killer whales to switch prey types given the high initial abundance of sea lions and the small number of killer whales in the Aleutians. The SE Alaska model also assumed a strong predator relationship between killer whales and sea lions, but the low numbers of sea lions could only have constituted a small proportion of the killer whales' diet in the 1960s. Furthermore, there was no incentive for killer whales to switch to sea lions at any given time in the simulations, since there were always enough small mammals in the ecosystem model for them to consume.

Models that considered only the predator–prey relationships between transient killer whales and Steller sea lions yielded different conclusions about the potential impact of killer whales. Considering the central and eastern Aleutians, Springer et al. (2003) used a ratio of transient killer whales to sea lions of about 0.0025, which is similar to that of our SE Alaska model and 10 times larger than that calculated for our Aleutians model. Although Springer et al. (2003) were not explicit on the proportion of sea lions in killer whale diets, they suggested that it would take only a small change in diet to cause the sea lion decline. In contrast, our model results suggest that it would take a large change in diet to have provoked the decline. Other attempts to test the sequential megafaunal collapse theory have also failed to find support for the assumptions and conclusions drawn by Springer et al. (2003) (see DeMaster et al. 2006; Trites et al. 2006*a*; Wade et al. 2006).

Barrett-Lennard et al. (1995) modelled the effect of killer whales on Steller sea lions using a low proportion of sea lions in the killer whales' diet (10%–15%), an estimate of 258 killer whales, and a maximum of 200 000 sea lions in the entire Northeast Pacific (Aleutian Islands to northern Washington coast), for an abundance ratio of 0.001. They found that depending on the functional predator–prey relationship (type II or III), the number of killer whales that would maintain the sea lion population constant would vary from 200 to 275 killer whales given an initial population of 200 000 sea lions. Our model results showed that when sea lion numbers declined in the Aleutians, predation mortality increased, although the importance of each species prey in the killer whales diet shifted slightly. In addition, our model results suggested that a low proportion of sea lions in the killer whale diet would not have been sufficient to cause a decline in killer whales in the 1990s. Barrett-Lennard et al. (1995) favoured the type III functional response based on observations that killer whales can specialize to hunt other species, and sea lions can use rookeries as refuge. Our model produces a type III functional response because sea lions alter their behaviour and remain in refuges for larger periods as their abundance decreases. However, our model did not explicitly consider a change in killer whale predatorial behaviour (though this would be straightforward to include).

Using the 1950 Bering Sea ecosystem model (Trites et al. 1999) and Ecosim predictions, a National Research Council committee was unable to fit the observed abundance trajectories for fish and Steller sea lions (National Research Council 2003). The National Research Council committee did not use any of the Pacific production indices (e.g., PDO) to force primary production anomalies (although they did use a forcing function estimated by Ecosim) and were unable to test the hypothesis of increased killer whale predation because they did not consider transient killer whales separately. Nevertheless, their modelling exercise showed that fishing and sea lion killings alone were insufficient to explain the decline.

The two ecosystems we considered did not allow us to examine the relationship between the increase in Pacific herring and walleye pollock because walleye pollock fishing was not important in these two areas. Further work should concentrate on the Bering Sea and the central GOA to examine these questions. The ecosystem modelling was successful at integrating climate, competition, fisheries, and predation as potential causes of change in each ecosystem. It appears that climate impacted several species in both ecosystems, including species such as Atka mackerel and Pacific herring that form an important part of the Steller sea lion diet. Thus, change in ocean productivity appears to have had a major, indirect effect on sea lions. Fishing was important on target species and dominated the definition of biomass trends for several of them (e.g., sablefish and Pacific ocean perch) but did not seem to change the structure of the ecosystems. The direct effects of fishing appeared as a secondary factor in determining sea lion abundance in both ecosystems, although simulation results suggest that killer whale predation increased as feeding time increased in SE Alaska. Given the very large initial numbers of sea lions in the Aleutians, killer whale predation seems to not have played a role in the sea lion decline until the mid-1980s when sea lion numbers were substantially lower.

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Tribributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers

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Abstract: Lotic ecosystems are made up of numerous tributary streams forming a complex branching network. The point where smaller tributaries flow into larger rivers, or tributary junctions, may be sites in the network where spatial discontinuities or "hot spots" are created and maintained, because small streams funnel important materials captured from the surrounding landscape and carry them by gravity downstream. We hypothesized that habitat complexity, environmental productivity, and abundance of primary consumers and predators peak in mainstem rivers at or downstream of tributary junctions. We conducted surveys in three river basins and 13 reaches to examine interdependence between tributary streams and the larger rivers they enter. Wood abundance and volume, variability in median substrate size (i.e., substrate heterogeneity), concentrations of nitrogen and phosphorus in water, algal biomass, and abundance of consumers and predators peaked with a higher frequency at or downstream of tributary junctions. For several variables, the size of the tributary relative to the main stem contributed to the strength of tributary affect. These findings suggest that some tributary streams have fundamental effects on the larger rivers they enter. We argue that maintaining the integrity of connections among and between ecosystems is essential for promoting habitat complexity and community structure within river networks.

Résumé : Les systèmes lotiques sont formés de nombreux tributaires réunis en un réseau dendritique complexe. Les points de jonction des tributaires, où les tributaires de taille inférieure se jettent dans les rivières de taille plus importante, peuvent générer et maintenir des discontinuités ou des « points chauds » dans le réseau; en effet, les petits cours d'eau accumulent des matériaux importants provenant du paysage environnant et les charrient vers l'aval par gravité. Nous formons l'hypothèse selon laquelle la complexité de l'habitat, la productivité du milieu et l'abondance des consommateurs primaires et des prédateurs atteignent toutes des maximums dans les cours principaux aux points de jonction des tributaires ou juste en aval. Nous avons mené des inventaires dans trois réseaux hydrographiques et 13 sections de cours d'eau pour évaluer l'interdépendance entre les tributaires et la rivière plus importante qu'ils rejoignent. Nous observons que les maximums d'abondance et de volume de bois, de variabilité de la taille moyenne du substrat (c'est-à-dire de l'hétérogénéité du substrat), des concentrations d'azote et de phosphore dans l'eau, des biomasses des algues et des abondances des consommateurs et des prédateurs se situent plus fréquemment aux points de jonction des tributaires ou juste en aval. Pour plusieurs des variables, la taille du tributaire par rapport au cours axial de la rivière contribue à augmenter l'effet du tributaire. Ces données laissent croire que certains tributaires ont des effets radicaux sur les rivières plus grandes qu'ils alimentent. Nous croyons que le maintien de l'intégrité des interconnections à l'intérieur des écosystèmes et entre les écosystèmes est essentiel pour favoriser la complexité des habitats et la structure des communautés dans les réseaux de rivières.

[Traduit par la Rédaction]

Introduction

Discontinuities, or transition zones, are ubiquitous in nature (Naiman and Décamps 1997) and are potentially important in maintaining biodiversity (Naiman et al. 1988; Polis et al. 1997). For example, river networks contain numerous discontinuities, with streams entering and leaving lakes (Richardson and Mackay 1991), rivers mixing with floodplains (Amoros and Bornette 2002; Sabo and Power 2002), two rivers intersecting (i.e., tributary junction or confluence) (Rice

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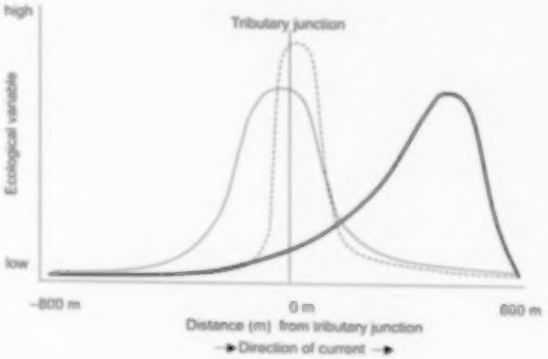
et al. 2001), and rivers entering oceans (Darnaude et al. 2004). The movement of water, energy, nutrients, sediment, wood, and organisms from one distinct habitat to another may create sites of high habitat complexity, biological productivity, and diversity at these discontinuities or "hotspots" (Polis et al. 1997; Power and Dietrich 2002). Unfortunately, we know relatively little about the formation and location of discontinuities in river networks and whether they are associated with habitat complexity, productivity, or community structure (Fisher 1997; Power and Dietrich 2002; Benda et al. 2004).

Until recently, conceptual models of aquatic systems have often downplayed or ignored the importance of discontinuities. For the last 25 years, the field of aquatic ecology has generally relied on the River Continuum Concept, which posits that controls on aquatic systems result in linear patterns of abundance and diversity as one proceeds downstream (Vannote et al. 1980). Although patterns in some factors, in particular energy inputs, support predictions of the River Continuum Concept (Minshall et al. 1983), results from other studies have not supported biodiversity patterns predicted by this model (Winterbourne et al. 1981). Moreover, considerable evidence is mounting that aquatic habitat complexity and productivity are not solely longitudinal functions of river length, but are instead discontinuously distributed in river networks (Rice et al. 2001; Poole 2002; Benda et al. 2004). In this paper, we examine whether one potential source of discontinuities in aquatic systems — tributary confluences — create gradients in productivity and diversity.

A conceptual model recently proposed by Benda et al. (2004), which couples disturbance regime with network structure, suggests that habitat complexity is generally greater around tributary confluences; therefore, biological diversity and productivity should peak at these points. Geomorphologists have long appreciated that unique changes in physical habitat occur at tributary confluences (Benda et al. 2004, and references cited therein). Only a few studies, however, have explicitly examined the effects of tributaries on the distribution and abundance of organisms of the larger rivers they enter and the mechanisms driving these patterns (Bruns et al. 1984; Stevens et al. 1997; Rice et al. 2001). Rice et al. (2001) found that invertebrate taxa richness peaked at tributary confluences and speculated that this pattern was in response to greater habitat diversity.

We build upon these earlier studies examining the role of small streams on larger rivers by assessing patterns in a range of environmental attributes that are known to affect species' abundance and distribution. Our study is unique in that we examined multiple physical, chemical, and biological endpoints, including algal biomass, density of large invertebrate consumers, and density and diversity of benthic and water column fishes. Testing this hypothesis is a challenge, primarily because potential nonlinear effects of tributaries on their main stems might result in several possible patterns across mainstem gradients (Fig. 1). We therefore examined tributaries that ranged in size relative to the main stems they enter in four different basins and used surveys that covered an intermediate spatial scale (10^1–10^5 km). These design elements have been proposed to be important for understanding factors controlling fish assemblages (Fausch et al. 2002). We sampled an extensive range of ecological variables including multiple taxa that allowed us to identify patterns in habitat complexity, water chemistry, and stream organisms. Specifically, we tested the hypothesis that tributary streams increase habitat complexity and resource abundance of the larger rivers they enter and consequently result in peaks of biological production, abundance of multiple taxa, and fish diversity at and below tributaries.

Fig. 1. Hypothetical relationships of nonlinear patterns in ecological variables (i.e., chemical, physical, or biological) resulting from tributary inputs upon a mainstem reach. Distances from the tributary junction or "0 m" (solid vertical line) increase traveling upstream or downstream in metres. The broken line indicates that tributaries may cause a localized effect resulting from various inputs (e.g., nutrients). The solid line shows that tributaries might also have effects both upstream and downstream on the main stem if inputs (e.g., hyporheic flow or gravel) are spread across an alluvial fan. The thick line indicates that tributaries might also have effects far downstream if inputs are large or result in greater habitat complexity.



Materials and methods

Study sites

Our surveys were conducted at the Cedar River, Taylor Creek, Bacon Creek, and Finney Creek, which are located in the foothills of the Cascade Range mountains in western Washington, USA. This area is part of the Pacific Coastal ecoregion (Naiman and Bilby 1998), which is generally mild (minimum–maximum annual temperature = 4–15 °C; National Oceanic and Atmospheric Administration (NOAA) 2005), with wet (minimum–maximum annual precipitation = 145–203 cm) winters and a pronounced summer dry season. Upland and riparian vegetation are dominated by the conifers western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Franklin and Dyrness 1969). Dominant broadleaf riparian species are primarily black cottonwood (*Populus trichocarpa* Torr. & A. Gray), red alder (*Alnus rubra* Bong.), vine maple (*Acer circinatum* Pursh), and salmonberry (*Rubus spectabilis* Pursh).

These basins were primarily forested, with Bacon Creek and Finney Creek tributary to the Skagit River (Fig. 2; Table 1).

Fig. 2. Map of study streams: (*a*) Skagit River sites, (*b*) Cedar River and Taylor Creek sites. Circles represent study reaches, with the small dot within each circle representing location of tributary–mainstem confluence.

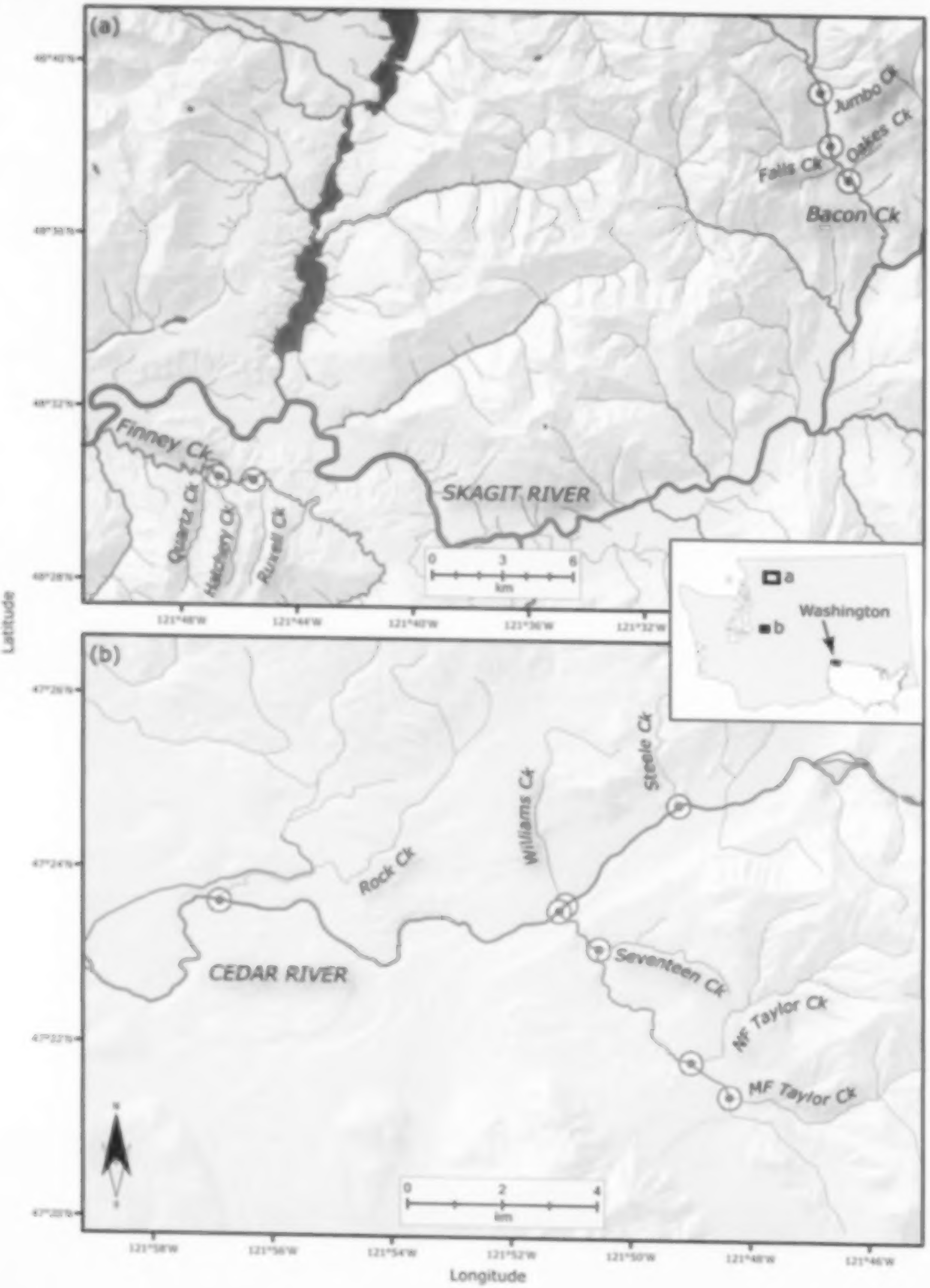

(a)
Jumbo Ck
Oakes Ck
Falls Ck
Bacon Ck
Finney Ck
SKAGIT RIVER
Quartz Ck
Hatchery Ck
Russell Ck
0
3
6
km
48°40'N
48°36'N
48°32'N
48°28'N
121°48'W
121°44'W
121°40'W
121°36'W
121°32'W
a
b
Washington
Latitude
(b)
Steele Ck
Williams Ck
Rock Ck
CEDAR RIVER
Seventeen Ck
MF Taylor Ck
MF Taylor Ck
N
0
2
4
km
47°26'N
47°24'N
47°22'N
47°20'N
121°58'W
121°56'W
121°54'W
121°52'W
121°50'W
121°48'W
121°46'W
Longitude

Table 1. Tributary and mainstem areas, ratio of tributary to mainstem area, reach lengths, average channel depth, channel width, and slope for each tributary–mainstem confluence.

Main stem	Tributary	Tributary area (ha)	Mainstem area (ha)	Tributary/ main stem	Reach length (m)	Average channel depth (cm)	Average channel width (m)	Slope
Finney	Ruxell	481	10 382	0.046	680	35	16	0.8
	Hatchery*	454	11 100	0.041				
	Quartz*	1 053	11 566	0.091	840	52	16	1.5
Bacon	Jumbo	206	8 734	0.024	800	76	20	1.6
	Falls	1 466	9 530	0.15	920	66	21	1.5
	Oakes	324	11 715	0.028	840	75	21	1.8
Cedar	Steele	281	22 814	0.012	800	77	22	1.0
	Williams	600	23 800	0.025	800	95	26	0.6
	Taylor	4 431	24 408	0.18	800	95	29	0.6
	Rock	1 484	30 121	0.05	800	83	33	0.6
Taylor	South Fork	548	1 578	0.35	240	27	6	1.7
	North Fork	1 103	3 799	0.49	360	36	10	2.0
	Seventeen	530	3 799	0.14	500	51	12	1.5

*Confluences were so close that we combined reaches.

Finney Creek is located on private timberland, while Bacon Creek is located on US Forest Service and National Park Service property. The Cedar River and Taylor Creek are located within the city of Seattle's watershed, which is currently managed as a conservation area. Chester Morse Lake, a water storage reservoir, is ~4 km upstream of the Steele Creek – Cedar River confluence. Because there were no pre-dam assessments, we are unable to determine whether there have been impacts on stream habitat below the reservoir. Potential impacts of dams include changes in water velocity, stream depth, substrate composition, and cover for fish. We argue, however, that reservoir operations have not overwhelmed the impact of tributary streams on the Cedar River main stem. The flow regime below the reservoir is similar to flow patterns observed in nearby unregulated rivers (United States Geographical Survey (USGS) 2006); therefore, impacts on flow are likely minimal. Because Chester Morse Lake is on a site of a natural lake and the reach downstream of the dam is a bedrock canyon, neither streambed degradation nor armoring occurs downstream (Seattle Public Utilities 2000). Moreover, any longitudinal impacts on sediment characteristics due to the dam in the sections we surveyed were minimal because the first tributary is relatively far from the reservoir (~4 km). Finally, none of the tributaries are regulated. Without data, however, there remains the possibility that the reservoir may impact downstream habitat, thereby confounding effects of tributaries on the main stem.

To examine gradients in environmental characteristics of mainstem rivers, we conducted detailed surveys on the physical, chemical, and biological attributes at 13 tributary junctions. We surveyed four tributary–mainstem reaches on the Cedar River (July–August 2002) and three on Taylor (August 2002), Finney (July–August 2003), and Bacon creeks (August–September 2003). These are clear, cool, rocky bottom streams, with mainstem sites relatively open because of their width, whereas tributaries are primarily shaded. The area of our mainstem sites ranged from 1578 to 30 121 ha, while the ratio of tributary to mainstem area ranged over an order of magnitude from 0.046 to 0.49 (Table 1).

Survey protocols

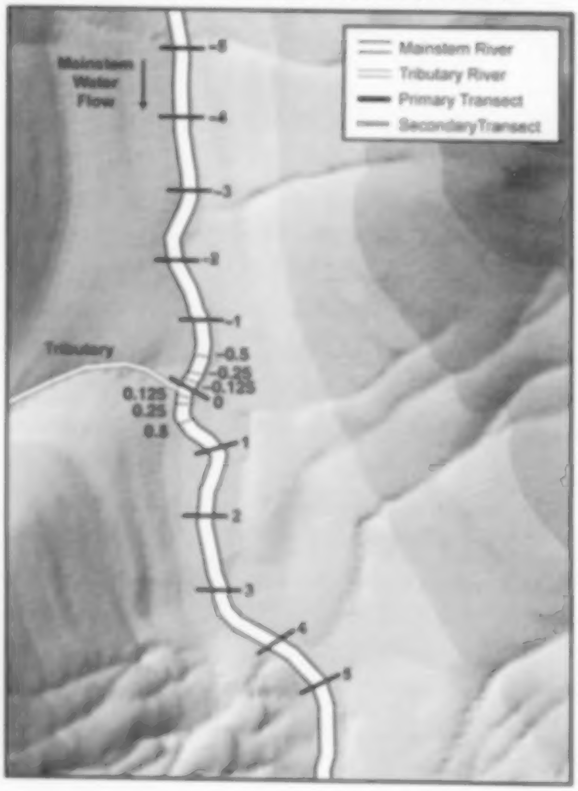
Reach delineation

Our survey design and methods were based on a standardized approach developed by the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program (Kaufmann 2002). Reach lengths were 40 times the average wetted width of the main stem during our surveys and ranged from 240 to 920 m (Table 1). Each reach was divided into 11 equally spaced transects that were perpendicular to water flow, with six primary transects upstream and five transects downstream of each tributary (Fig. 3). Distances between transects differed among the 13 tributary–mainstem reaches, because the distance between transects was shorter for narrower channels and longer for wider channels. To standardize this distance across the 13 tributary junctions for analysis and graphical presentation, we divided the distance between each transect and the tributary by the intratransect distance. We called this distance between transects as the standardized distance unit (SDU), ranging in value from –5 to 5.

To determine the location of each transect, we used the upstream extent of alluvial fans at the mouth of each tributary to place the initial primary transect. The position of remaining primary transects were then dependent on this location. We also placed secondary transects within each reach, which were 12.5%, 25%, and 50% of the distance between primary transects. Secondary transects were located between 1 and –1 SDU and ranged from 0.5 to –0.5 SDU. The purpose of these transects was to determine if there were small-scale patterns in water temperature, algal biomass, nutrient chemistry, and large invertebrate and sculpin (*Cottus* sp.) abundance, resulting from tributary confluences. Because we hypothesized these small-scale spatial patterns would dissipate relatively quickly as one moved away from the tributary junction and maintaining this sampling intensity between all transects was logistically a challenge, we confined these secondary transects to between 1 and –1 SDU.

Quartz and Hatchery creeks entered Finney Creek about 50 m apart, creating a large floodplain complex. Because

Fig. 3. Survey design used for this study. Primary transects were 5 though –5, with the 0 transect located immediately upstream of the tributary–mainstem confluence. Secondary transects (0.125 to –0.125) were used to sample nutrients, water temperature, algae, and *Dicosmoecus gilvipes* and sculpin (*Cottus* sp.) density.



these two tributaries were so close together, it was difficult to determine whether observed patterns were related to individual tributaries. Therefore, we treated this tributary complex as one reach with one tributary input.

Physical and chemical measurements

Throughout each study reach, we estimated wood volume, substrate size, canopy cover, and nutrient levels. Pieces of wood >0.1 m in diameter and >1.0 m in length that were in contact with the wetted channel were counted continually from transect 5 through –5. Wood abundance was converted to volume within each size class using the following formula: wood volume (m^3) = 3.14 r^2 l, where r equals the radius and l the length of each log in each size class. These values were then summed across size classes to determine minimum wood volume per transect. To determine substrate size and heterogeneity (coefficient of variation), pebble counts were conducted at each primary transect. We assigned 100 to 300 rocks selected across each transect to different size categories using the intermediate axis and a gravelometer (Wildco Supply, Buffalo, New York). Individual stones were selected by picking up the rock located directly in front of the big toe of the sampler's boot. One step was taken from this point where another rock was selected until 100 to 300 rocks were measured. Each pebble count began and finished at the stream edge to minimize bias introduced by location within transects. Canopy cover was measured at primary transects using a spherical densiometer. At each transect, measurements were taken in four directions (facing the bank, upstream, downstream, and facing towards the opposite bank) in the middle of the channel and once at each bank facing the stream.

Grab water samples were collected from primary and secondary transects on the main stem and tributary. These samples were analyzed for total nitrogen and phosphorus, dissolved nitrate and nitrite, ammonia, and soluble-reactive phosphorus (College of Oceanography, University of Washington, Seattle, Washington).

Biological measurements

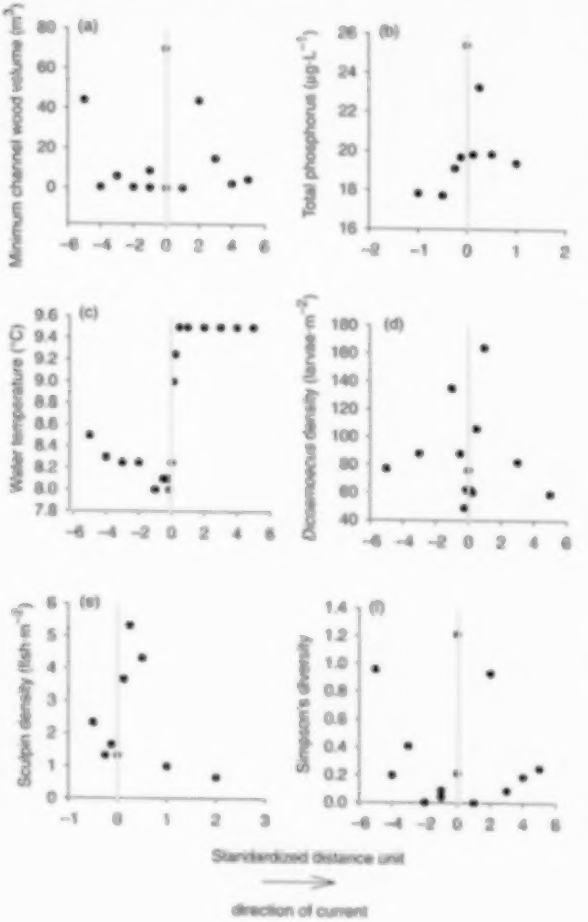
Ambient periphyton biomass was determined by processing fist-sized rocks (~8 cm wide) collected from three (left, middle, and right side of transect) locations across each transect. To determine periphyton and algal biomass, rocks were scrubbed thoroughly with a brush and rinsed with distilled water. This slurry was split into equal subsamples and analyzed for periphyton biomass as ash-free dry mass (AFDM) and chlorophyll *a* (see Kiffney et al. 2003 for further details). To estimate the area of each stone, we used calipers to measure the x, y, and z axes of each stone; this area was then divided by two because we assumed most of the algal biomass accrued on the upper rock surface.

To characterize benthic fauna, surveys were conducted at primary and secondary transects. A square plastic (polyvinyl chloride pipe) frame (0.25 m^2 area) weighed down by sand within the pipes was carefully placed on the stream bottom at three locations (left, middle, and right side) across each transect. Within each quadrat, we counted and identified sculpin, a small benthic fish, and large, cased caddisflies (primarily *Dicosmoecus gilvipes*). Placing this frame on the stream bottom likely led to the emigration of small, mobile insects, such as mayflies (Order Ephemeroptera); however, we were most interested in counting large, immobile, and easily identifiable taxa.

Continuous snorkel surveys from transect 5 through –5 were conducted at each reach to determine relative abundance, composition, and size class (total length <50 mm = class 1, 51–100 mm = class 2, 101–150 mm = class 3, 151–200 mm = class 4, 201–250 mm = class 5, >251 mm = class 6) of stream salmonids (*Oncorhynchus kisutch*, *Oncorhynchus mykiss*, *Oncorhynchus clarkii clarkii*, *Oncorhynchus tshawytscha*, *Oncorhynchus nerka*, *Oncorhynchus gorbuscha*, *Prosopium williamsoni*) and bull trout (*Salvelinus confluentus*) (Wydoski and Whitney 2003). Surveys were conducted within a 2-week period to minimize affects of seasonal migration on abundance. Depending on channel width, one to four snorkelers moved upstream in unison from one transect to the next (Thurow 1994). To minimize double counts of fish, each snorkeler was assigned a lane; any fish that moved between lanes (mostly large individuals >150 mm total length) was assigned to one person through communication among snorkelers. Snorkelers relayed number, identity, and size class to recorders on the bank.

We recognize there are sampling issues with using snorkel surveys to estimate abundance (Thompson 2003), but this

Fig. 4. Scatterplots of response measure values vs. standardized distance units (SDU) for (*a*) minimum channel wood volume at the Quartz–Hatchery–Finney creeks confluence, (*b*) total phosphorus concentrations at the Rock Creek – Cedar River confluence, (*c*) water temperature at the Seventeen Creek – Taylor Creek tributary, (*d*) *Dicosmoecus gilvipes* density at the Ruxell Creek – Finney Creek confluence, (*e*) sculpin (*Cottus* sp.) density at the Steele Creek – Cedar River confluence, and (*f*) Simpson's reciprocal index of fish diversity at the Quartz Creek – Finney Creek confluence. The shaded, vertical line represents the location of the tributary–mainstem confluence.



approach was used for the following reasons: (*i*) reach lengths were long (mean = 698 m) and two rivers were large, deep, and fast (Cedar River and Bacon Creek), which made electroshocking logistically difficult; (*ii*) water clarity of these rivers was high (~5 m) and there were relatively few species, with most having distinct characteristics making visual detection and identification of fish relatively easy; (*iii*) we wanted to use the same method across habitat types and stream sizes; and (*iv*) we were interested in estimating relative abundances across these strata. Because we used the same methods across transects, reaches, and streams, we suggest that this approach was suitable for addressing our hypotheses. Moreover, observer bias was minimized, because two individuals (Kiffney and Greene) conducted 90% of fish counts.

We used two measures to estimate the diversity of stream fishes. The number of fish species in these systems is low; however, the number of size classes within a species is relatively high as a result of complex life histories within Salmonidae. For example, a large pool may contain two species of salmon or trout, but support three to four size classes of each species. We assumed that this species – size class diversity was analogous to species diversity, especially within a stream, because a diverse suite of life stages within a pool may be functionally different from a pool with only one to two size classes. Therefore, as one measure of fish diversity, we summed the number of size classes within each species to determine species × size class diversity. For instance, one reach may have two species (cutthroat and rainbow trout), with each species having four size classes, so the species × size class diversity for this reach equals eight. Likewise, if one species had two size classes and another had four size classes, the diversity index would equal six. We also used a standard diversity index, Simpson's reciprocal index of diversity (D^{-1}), to measure species diversity ($D = \Sigma(n\,N^{-1})^2$), where n is the total number of organisms of a particular species, and N is the total number of organisms of all species (Magurran 1988).

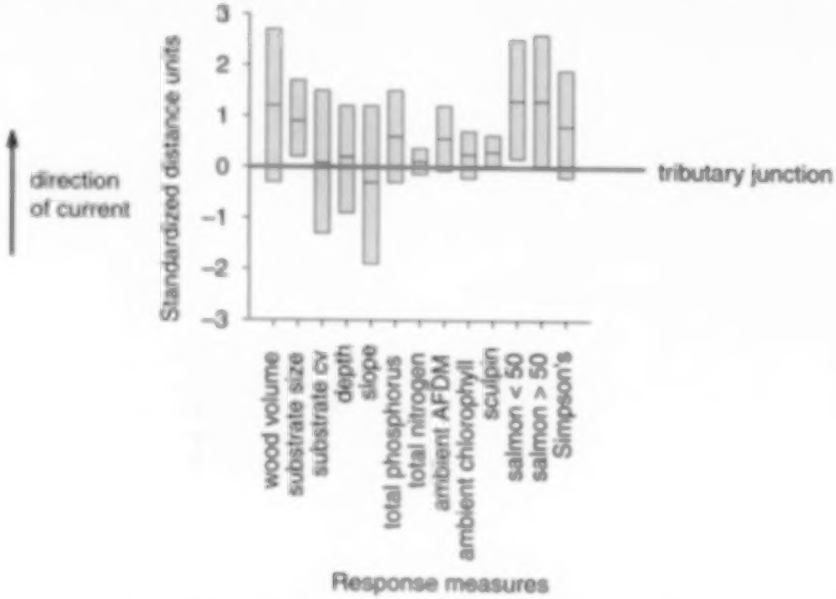
Statistical analysis

Sample units were transects, so multiple samples collected within individual transects were pooled (e.g., three rock samples were collected per transect for algal biomass; these values were pooled to determine the mean value for each transect).

The nonlinearity in ecological patterns along each reach made it a challenge to quantify tributary impacts. Therefore, we focused on the location of peak values for each response variable as determined by measurements at each transect to determine whether tributary junctions created discontinuities in ecological measures. We plotted mean ± 95% confidence intervals for the location or SDU for the peak value for each response measure. Because tributary effects on mainstem habitat can occur upstream and downstream of the tributary confluence (Benda et al. 2003), we predicted that, on average, peak values for these response measures would occur at or downstream of each tributary junction (Fig. 1).

Because there was considerable variation in physical, chemical, and biological attributes among basins, and almost every variable we measured revealed major interbasin differences, we also examined tributary affects by calculating z scores for sample data of points relative to other points within a given basin. The z score reveals how many standard deviations away from the mean a score resides, with a positive value indicating a z score above the mean and negative value below. In addition to standardizing data across basins, z scores provide a convenient way to test for significant peaks at and below tributary junctions. Using z tests, we examined whether these peaks surpassed the critical z score (assuming a two-tailed test) for significance when compared with other values measured within that basin. This test essentially asked whether a peak value associated with each study reach was within the range of variation expected for the basin. Hence,

Fig. 5. Mean ± 95% confidence intervals for the location (standardized distance units, SDU) of peak values for physical, chemical, and biological response measures. AFDM, ash-free dry mass.



for any single variable, each of the 12 tributary junctions constituted a z test. We then used histograms that summed the frequency of peak values within bins defined by SDUs to assess the overall pattern of peak values as a function of distance from tributaries. Before analyzing peak values using z scores, we examined whether the data were normally distributed using the Kolmogorov–Smirnov test. When this assumption was violated, we used the logit transformation for percentage data and log transformations on other types of data to normalize their distributions.

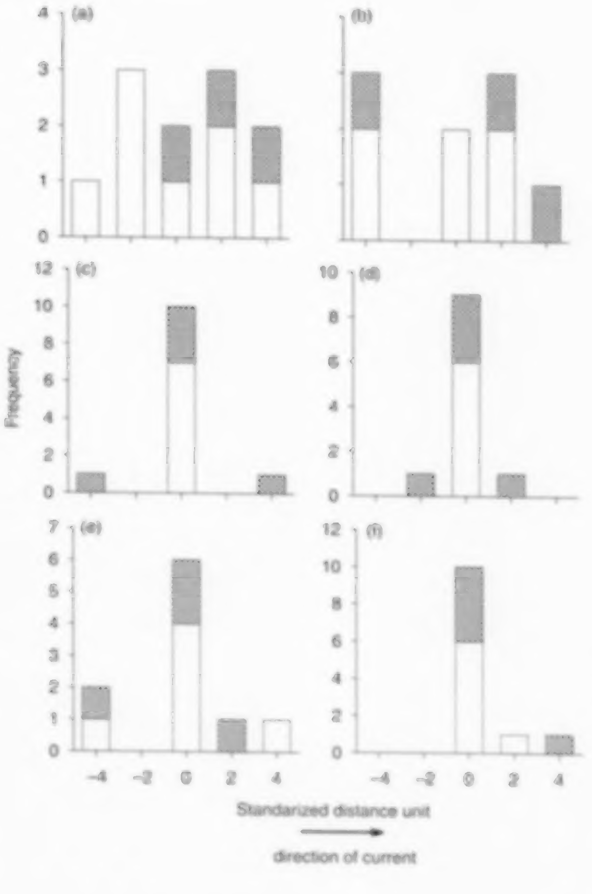
Results

There was significant spatial variation in the distribution of sample values, especially for physical responses and salmonid abundance; however, surveys revealed distributions that were generally consistent with patterns in Fig. 1. Specifically, we observed peaks in a number of response measures at tributary confluences, with values declining with distance from this point. For instance, the Quartz–Hatchery–Finney creeks confluence was highly complex, with in-channel wood peaking around the tributary–mainstem confluence (Fig. 4*a*). In general, concentrations of limiting nutrients were higher in tributaries, which in some cases translated into higher nutrient concentrations downstream of confluences, especially in the Cedar River (Fig. 4*b*). We also observed that tributary streams influenced water temperature of mainstem rivers. Water temperature downstream of the Seventeen Creek – Taylor Creek confluence increased sharply by ~1.4 °C (Fig. 4*c*). In some cases, we also observed higher densities of insect consumers and predators below tributary streams. Density of the large cased caddisfly, *Dicosmoecus gilvipes*, was about two–three times higher near the Ruxell Creek – Finney Creek confluence compared with transects further away (Fig. 4*d*). Sculpin abundance in the Cedar River was also tightly linked to tributary junctions, as density was about two times greater near the Steele Creek – Cedar River confluence than further away (Fig. 4*e*). Although salmon and diversity responses were generally more variable than productivity or chemical measures, Simpson's index of fish diversity peaked at the Quartz–Hatchery–Finney creeks confluence (Fig. 4*f*). Patterns in fish diversity at this tributary–mainstem confluence largely tracked volume of in-channel wood (Fig. 4*a*).

When analyzed collectively, we also observed patterns consistent with our hypothesis that tributary streams create environmental gradients. On average, the mean location of almost all measures occurred at or downstream of tributary junctions (Fig. 5). For example, a higher frequency of peaks in wood volume and median substrate size occurred at 1 SDU, with substrate heterogeneity and stream depth occurring about 0 SDU. Peaks in total nitrogen, phosphorus, ambient periphyton AFDM, chlorophyll a, and sculpin abundance occurred from 0.1 to 0.5 SDU and were less variable than physical or other fish measures. Salmon abundance and diversity peaked at 1 SDU, which was similar to wood volume and substrate size. In almost all measurements of salmon density and diversity, the 95% confidence intervals for locations of peak values did not overlap the 0 SDU line. Hence, peak values of these measures were significantly downstream of tributary junctions.

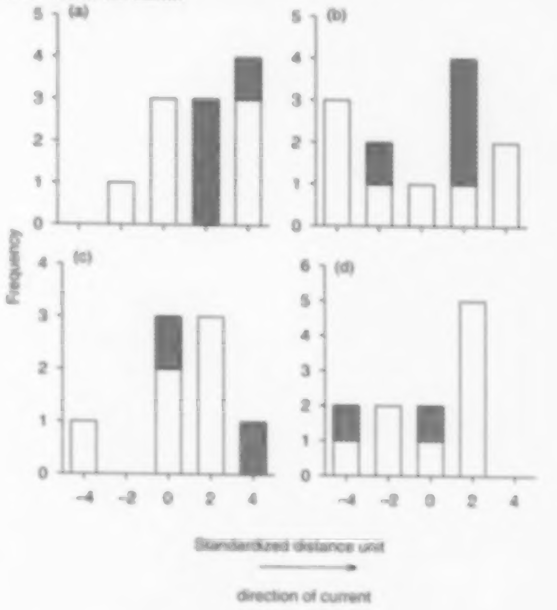
The z-score analysis provided further evidence for creation of ecological discontinuities by tributary streams (Fig. 6). Significant peaks in wood volume (Fig. 6*a*) and substrate diversity (Fig. 6*b*) occurred more often 0–4 SDU downstream of tributary junctions than elsewhere. Measures of productivity were tightly linked with tributary junctions, although this result may be a function of higher sampling frequency between 1 and −1 SDU. Total phosphorus generally

Fig. 6. Spatial distributions of peak values for (*a*) minimum volume of channel wood, (*b*) substrate diversity (defined as the coefficient of variation (%) of median substrate size), (*c*) total phosphorus ($\mu g \cdot L^{-1}$), (*d*) total nitrogen ($\mu g \cdot L^{-1}$), (*e*) ambient periphyton ash-free dry mass ($\mu g \cdot cm^{-2}$), and (*f*) ambient chlorophyll *a* biomass ($\mu g \cdot cm^{-2}$) measured within 12 study reaches in four river basins. Within each panel, each datum represents the spatial location of the peak within the study reach, with the tributuary junction located at *zero*. Hence, each bar represents the frequency of peaks measured within five reach sections: (*a*) at or between transects −4 and −5 = −4, (*b*) at or between transects −2 and −3 = −2, (*c*) at or between −1 and 1 = 0, including all secondary transects, (*d*) at or between 2 and 3 = 2, and (*e*) at or between 4 and 5 = 4 (refer to Fig. 3 for position of transects). Hatched portions of bars represent data surpassing the 0.05 level of significance when those points were compared with others within its basin.



peaked 0–1 SDU (Fig. 6*c*), while total nitrogen peaked 0–0.5 SDU (Fig. 6*d*). Ambient AFDM peaked at 0–1 SDU (Fig. 6*e*), while ambient chlorophyll *a* peaked more often between −0.5 and +0.5 SDU (Fig. 6*f*). These variables had significant peaks associated with tributary inputs in 2–4 of the 12 reaches.

Fig. 7. Spatial distributions of peak values for (*a*) estimates of salmon density ≤50 mm in total length ($fish \cdot m^{-3}$), (*b*) estimates of salmon density ≥50 mm in total length ($fish \cdot m^{-3}$), (*c*) species × size class, which represents size class diversity, and (*d*) Simpson's reciprocal index of diversity measured within 12 study reaches in four river basins. Within each panel, each datum represents the spatial location of the peak within the study reach, with the tributuary junction located at *zero*. Hence, each bar represents the frequency of peaks measured within five reach sections: (*a*) at or between transects −4 and −5 = −4, (*b*) at or between transects −2 and −3 = −2, (*c*) at or between −1 and 1 = 0, including all secondary transects, (*d*) at or between 2 and 3 = 2, and (*e*) at or between 4 and 5 = 4 (refer to Fig. 2 for position of transects). Hatched portions of bars represent data surpassing the 0.05 level of significance when those points were compared with others within its basin.



Patterns in salmon abundance in relation to distance from tributary junction differed by size class and taxa, but tended to peak below tributaries. Juvenile salmon (<50 mm total length) exhibited the strongest tributary-related effect, with peaks at or downstream of tributaries in 10 of the 12 reaches, four of which surpassed the level of significance (Fig. 7*a*). The pattern for larger salmonids (>50 mm in total length) was less clear, but significant peaks occurred more often within 2 SDUs downstream of tributaries (Fig. 7*b*). The number of species × size classes, one measure of diversity, peaked below tributaries in 7 of the 12 reaches we examined and showed particularly large peaks in two of these (Fig. 7*c*). Simpson's diversity showed a less robust tributary effect than other variables. Nevertheless, peaks in Simpson's diversity also occurred more often close to tributary confluences, with two observations occurring 0–1 SDU and five occurring 1–2 SDU (Fig. 7*d*) downstream of tributaries.

Our results confirmed significant ecological effects of tributaries in some but not all reaches for the variables we examined. We hypothesized that the magnitude of the tributary

Table 2. Pearson's correlation coefficents of variables with the relative tributary area, measured as the proportion of total basin area flowing into a study reach within the tributary.

Variable	Correlation coefficient
Large wood volume	0.72**
Substrate CV	0.60*
Velocity	0.22
Thalweg temperature	–0.45
Thalweg depth	0.29
Canopy cover	–0.54
Total phosphorus	0.85**
Total nitrogen	0.69**
Ambient ADFM	–0.10
Ambient chlorophyll *a*	0.42
Salmonid fry (≤50 mm) density	0.10
Larger salmonid (≥50 mm) density	0.03
Species × size classes	0.39
Simpson's index	–0.20

Note: Correlations were computed with z scores of variables and logit transformations of relative tributary area data. Substrate CV, substrate coefficient of variation; ambient AFDM, ash-free dry mass on rocks. *, $p < 0.1$; **, $p < 0.05$.

effect should be related to the percentage of the watershed above a reach that was within the tributary. We tested this by correlating peak z values in each reach with the proportion of watershed area in the tributary. We found significant correlations for three variables (Table 2) and trends in several others. These correlations tended to be saturating functions of relative tributary area, leveling off after the tributary contribution was greater than 10%–15% of the upstream watershed (Fig. 8).

Discussion

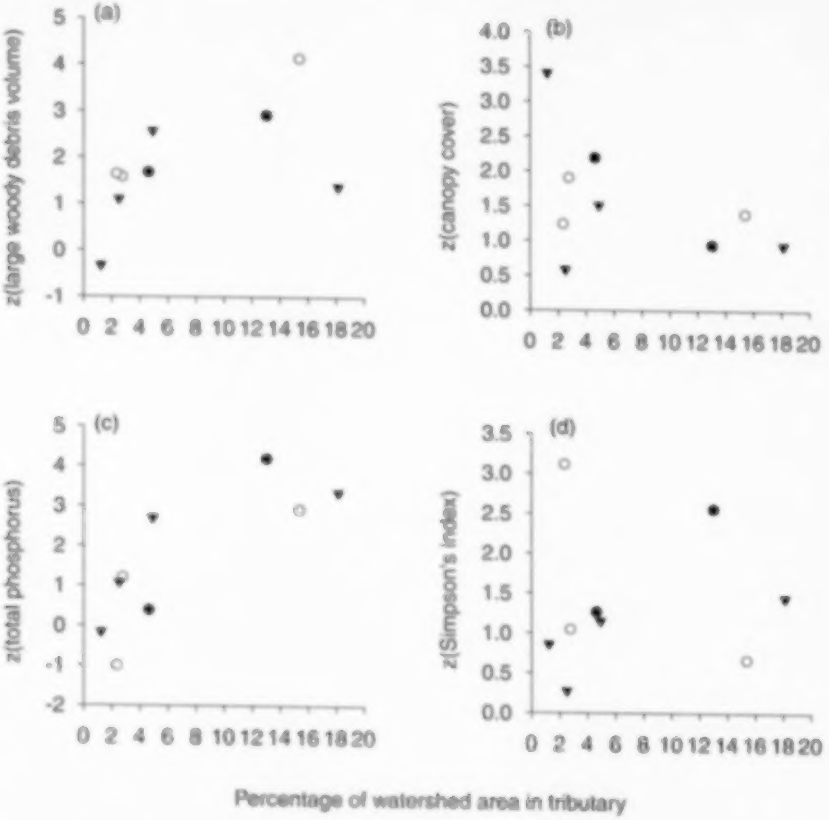
This study provides evidence that tributary junctions represented discontinuities in river networks. In general, physical, chemical, and biological attributes of our study reaches peaked at or downstream of these junctions. In most cases, the spatial distribution of values for our response measures was similar to hypothetical distributions, as well as distributions predicted from biogeochemical mechanisms operating in river systems. Furthermore, the mean location for peak values was at or below the tributary confluence. For example, total nitrogen and phosphorus and algal biomass generally peaked at or below tributary junctions. In addition, sculpin, large caddisfly, and juvenile salmonid abundance and species × size class diversity generally peaked at or slightly downstream of tributary junctions. We speculate that these patterns in biotic assemblages were in response to gradients in physical, chemical, and biological attributes partially created by tributary streams.

Tributary streams appeared to influence a variety of physical attributes of the mainstem rivers we examined, increasing morphological heterogeneity of receiving streams. Wood volume or abundance and median substrate size were generally higher at or downstream of tributary junctions. Other physical variables such as substrate heterogeneity and stream depth also peaked at or slightly below tributary confluences. The range in peak values for these physical measures was high, overlapping the 0 SDU line, which suggests other processes within our study reaches contributed to physical habitat heterogeneity. Disturbance regime, such as the timing, intensity, and frequency of floods that move wood and sediment, can affect the spatial distribution of these materials, potentially obscuring or redistributing tributary inputs. In some locations along Bacon and Finney creeks, steep valley walls border the river; local bank failure at these locations was a likely process contributing to the spatial distribution of sediment and wood. Bank failure was evident at the –6 SDU in the Quartz–Hatchery–Finney creeks reach, which contributed high volumes of wood to this transect. Other factors that can affect the strength of the tributary signal include the ratio of tributary to mainstem area, basin size and shape, drainage and confluence density, and network geometry (Benda et al. 2004). In addition, tributary effects on mainstem habitat can, in some cases, extend upstream of the confluence (Benda et al. 2003).

The resulting effects of tributaries on physical habitat and nutrients appear to create "biogeochemical hotspots" (McClain et al. 2003). These hot spots, defined as areas or patches that show disproportionately high reaction rates relative to the surrounding area, occur most frequently at boundaries or ecotones where two distinct landscape features meet, such as where two streams of distinct water chemistries intersect (McClain et al. 2003). Our results support this notion, as tributary streams created distinct gradients in water chemistry in mainstem rivers, which were generally nutrient-poor or oligotrophic. Long-term surveys in the Cedar River have consistently shown that concentrations of total and dissolved nutrients were higher in tributaries entering the main stem, with concentrations of these elements often remaining high downstream of tributaries (Kiffney et al. 2002). The importance of these inputs as agents of chemical change in the main stem, of course, is dependent upon the volume of water in the tributary relative to the main stem.

We offer two potential mechanisms to explain why some tributaries can create biogeochemical hot spots in mainstem rivers. Most of the tributaries we surveyed were strongly shaded by riparian forests, thereby limiting primary production and algal accrual (Hill et al. 1995; Kiffney et al. 2003). Low levels of primary production in tributary rivers may limit uptake of nutrients, so that tributary nutrients are transported into sunlit, mainstem rivers where they fuel primary production (Power and Dietrich 2002). Hill et al. (2001) found that dissolved nitrogen and phosphorus concentrations in stream water increased threefold, whereas aquatic primary production declined threefold coincident with leaf emergence. In addition, logging and natural disturbance events have led to riparian forests in many headwater streams of the Pacific Northwest to be composed mostly of red alder (Volk et al. 2003). Recent studies have demonstrated that streams draining red alder forests have higher levels of nitrogen and, in some cases, phosphorus than nearby streams dominated by conifers (Compton et al. 2003; Volk et al. 2003). Riparian red alder dominated many of the tributaries we surveyed, especially in the Cedar River. Therefore, these alder-

Fig. 8. Relationships of four variables as a function of the tributary area relative to the total amount of area upstream of each study reach. Different basins are represented by different symbols: solid circles, Finney Creek; open circles, Bacon Creek; solid triangles, Cedar River. One basin (Taylor Creek) was removed because of large differences of tributary stream order compared with the other three basins.

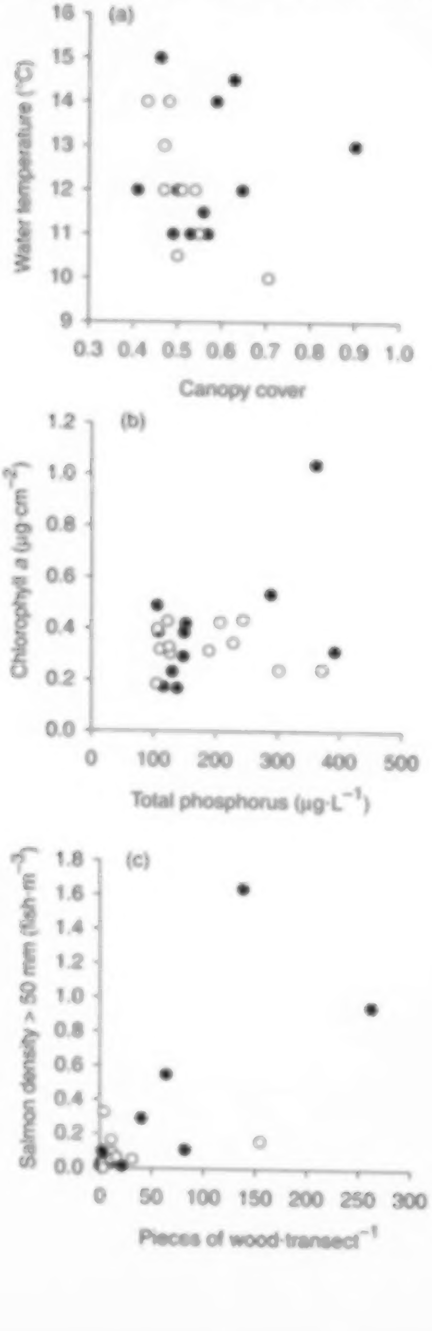


dominated tributaries may have high nutrient loads as a result of inputs of nutrient-rich leaf litter. If this is so, then the condition (e.g., community composition) of riparian forests in tributary streams may be tightly connected to the nutrient dynamics of downstream portions of the watershed.

In agreement with our predictions and potentially in response to peaks in nutrient resources, we observed that peaks in both periphyton AFDM and chlorophyll *a* occurred more often at or slightly downstream of tributary junctions. Algal biomass is extremely variable in both space and time in river ecosystems because of the variety of factors that affect algal communities (Biggs et al. 1998). For example, stream flow (Peterson and Stevenson 1992), water temperature (Bothwell 1988), nutrients (Peterson et al. 1993), biotic interactions (Hill et al. 1995), and habitat heterogeneity (Cardinale et al. 2002) contribute to variation in algal biomass, with these factors likely interdependent. Our study supports this view and suggests that tributary confluences may be locations within the river network where these factors interact to affect algal dynamics. For example, we found that total phosphorus was positively correlated with chlorophyll density when including all transects (P.M. Kiffney and C. Greene, unpublished data). We speculate that greater standing stocks of algal biomass may contribute to higher levels of consumer (i.e., *D. gilvipes* abundance) and predator biomass and abundance at tributary junctions by increasing resource supply.

Salmon abundance and diversity and sculpin abundance peaked downstream of tributary junctions, potentially in response to patterns of channel complexity and productivity. These data support the hypothesis that tributary junctions were nodal habitats for stream fishes, especially juvenile trout and salmon and sculpin, during summer. A number of interdependent mechanisms may contribute to these patterns. Tributary streams funnel detritus and nutrients into mainstem habitats, providing additional resources for invertebrates in the main stem that sculpin and drift-feeding fish consume. Invertebrates also drift out of headwater streams, providing food for fish residing in the main stem (Wipfli and Gregovich 2002). Wood abundance or volume is also an important predictor of fish abundance and diversity in streams (e.g., Johnson et al. 2005), as it serves a number of important functions for fish, such as providing refugia and a surface area for insect prey (Collier and Halliday 2000). We hypothesize that the combination of higher productivity and habitat complexity in mainstem rivers downstream of tributary junctions was partially responsible for distribution patterns of

Fig. 9. Examples of how tributary junctions can affect common relationships found in aquatic systems. In each panel, solid circles represent reach units downstream of tributary junctions, while open circles represent units at or upstream from confluences. (*a*) Input of warmer water from tributaries of Cedar River obscures the correlation of thalweg temperature and canopy cover. (*b*) In Bacon Creek, ambient chlorophyll density is correlated with total phosphorus downstream but not upstream of tributary junctions. (*c*) High densities of large (≥50 mm) salmonids were associated with logjams downstream of tributary confluences on Finney Creek, driving a significant salmonid – wood volume correlation.



stream fish. A recent study found that the diversity of electric fishes (Gymnotiformes) was higher in the mainstem Amazon River downstream of tributary rivers (Fernandes et al. 2004). These authors also hypothesized that tributary rivers carry nutrients and organic materials that provide food and habitat resources for electric fishes in the main stem.

Caveats and implications

Although we observed that gradients in physical, chemical, and biological attributes of river systems appeared to be centered on tributary junctions, other factors may account for this variation. This study was observational, which limits inferences because we could not disentangle mechanisms by which tributary junctions influence communities. Our study was confined to summer low-flow periods; therefore, the biological patterns we observed might be different during different seasons or years. For example, with the onset of the rainy season, fish in the main stem may migrate into tributary streams to escape high flow events (Brown and Hartman 1988).

Despite these issues, this study has a number of important implications for river ecology and conservation. One of the salient findings of this study is it illustrates the fundamental effects of tributary inputs on aquatic ecological processes. Moreover, these effects appear to increase as a function of the ratio of tributary to watershed area until this ratio reaches 15%. Given the strong patterns we found, researchers should consider tributary inputs as a large source of ecological variation. If areas downstream of tributaries have elevated levels of substrate, nutrients, and biological production, studies overlooking these spatial patterns might come to erroneous conclusions concerning common biological processes. We provide three examples that illustrate how this might occur (Fig. 9). In the first case (Fig. 9*a*), values measured downstream of tributaries obscured a common correlation between water temperature and canopy cover that was evident in values measured upstream (water temperature negatively correlated with canopy closure; Kiffney et al. 2003), which is significant if points at or downstream of tributaries are ignored ($r = -0.71$, $p < 0.05$). In the second case (Fig. 9*b*), there was no relationship between chlorophyll density and phosphorus level ($r = 0.02$, $p > 0.1$) upstream of tributaries, but this relationship was significant downstream of tributaries ($r = 0.60$, $p < 0.05$). The correlation across all sites is still significant ($r = 0.40$, $p < 0.05$), driven primarily by high values downstream of tributaries. A final example (Fig. 9*c*) shows a positive relationship between wood abundance and large salmonid abundance and illustrates how extreme values associated with tributaries might drive the strength of a correlation ($r = 0.60$, $p < 0.05$), which would not be significant in the absence of those data points ($r = 0.02$, $p > 0.1$). These patterns, therefore, illustrate that tributary inputs can obscure or drive study results if researchers ignored their importance in survey designs.

This study also supports the hypothesis that both productivity and habitat diversity were higher on mainstem reaches at or downstream of tributary junctions. The abundance of stream salmonids also peaked below tributary junctions, potentially in response to increased habitat heterogeneity and productivity. Based on the observed patterns of productivity and habitat diversity and the corresponding patterns of fish distributions, habitat heterogeneity appears to be the primary driver of fish communities. Habitat structure has also been found to be an important factor shaping reef fish communities (Syms and Jones 2000). However, fish likely take advantage of both productivity and habitat heterogeneity increases below tributaries by selecting downstream areas that conveys the benefits of both gradients.

We argue that this study has important implications for habitat conservation, as tributary steams appear to be important sources of habitat heterogeneity in river networks. The homogenization of habitat is thought to be one of the most important factors driving loss of biodiversity (Cardinale et al. 2002). A number of recent studies have shown that habitat diversity in the form of the abundance of wood, size and depth of pools, channel complexity, and substrate composition are higher where tributary streams enter mainstem rivers (Rice et al. 2001; Benda et al. 2004; Fernandes et al. 2004). In the Pacific Northwest and in other temperate regions, 75%–90% of all river kilometres are composed of tributary streams, resulting in watersheds with a highly branched appearance. If tributary streams are important drivers of habitat and biological diversity in mainstem rivers, the degradation of tributary habitat could have profound and lasting impacts on habitat and biodiversity of the rivers they enter.

Our study provides evidence to suggest that the connection between tributary and main stem was important for the flow of ecologically important materials (nutrients, sediment, wood) that contributed to habitat heterogeneity and biodiversity in the main stem. A variety of organisms, such as Pacific salmon, rely on a diversity of habitats within a watershed from headwaters to the estuary to maximize fitness. We speculate that maintaining the integrity of connections within river networks is critical to protecting and restoring salmon populations. Our findings, therefore, suggest that conservation plans for mainstem rivers include not only riparian buffers but also entire drainages of large ecologically important tributaries entering main stems.

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How to validate a length-based model of single-species fish stock dynamics

Kasper Kristensen, Peter Lewy, and Jan E. Beyer

Abstract: This paper validates a new length-based model of the dynamics of fish stocks or crustaceans by hierarchically testing statistical hypotheses and thereby investigating model complexity. The approach is based entirely on scientific survey data and on determination of the statistical distributions of the number of fish caught per haul in each length class. In our example, the negative binomial distribution is statistically accepted and linked to the population level through the new length-based model. The model is derived from the characteristics of continuous recruitment, individually based growth, and continuous, length-dependent mortality rates. Continuous recruitment with annually varying recruitment peaks and individually based growth was crucial for obtaining a model that could be statistically accepted. Natural mortality was estimated as well by the model. The model was applied to survey data for Atlantic cod (*Gadus morhua*) in the Baltic. Its simple generic nature, as well as the validation procedure, is useful in studying and understanding life history and stock dynamics.

Résumé : Notre travail valide un nouveau modèle de la dynamique des stocks de poissons basé sur les longueurs en testant des hypothèses statistiques de manière hiérarchique ; il examine ainsi la complexité du modèle. La méthode se base entièrement sur des données d'inventaire scientifique et sur la détermination des distributions statistiques des nombres de poissons capturés par trait de récolte dans chacune des classes de longueur. Nous acceptons dans notre exemple une distribution binômiale n égative et nous la relions au niveau de la population à l'aide du nouveau modèle basé sur les longueurs. Le modèle est dérivé des caractéristiques du recrutement continu, de la croissance individuelle et des taux de mortalité continus en fonction de la longueur. Le recrutement continu avec des pics de recrutement qui varient d'une année à l'autre et la croissance basée sur les individus sont de grande importance pour l'élaboration d'un modèle qui soit statistiquement acceptable. Le modèle estime aussi la mortalité naturelle. Nous avons appliqu é le modèle à des données d'inventaire de la morue franche (*Gadus morhua*) de la Baltique. La nature générique simple et la procédure de validation du modèle le rendent utile pour l'étude et la compréhension des cycles biologiques et de la dynamique des stocks.

[Traduit par la Rédaction]

Introduction

Validation is a vital part of the modelling process, since it is here the model is confronted with reality. How to make this confrontation in an objective way has often been neglected in studies of fish stock dynamics. In this paper, we present a statistical validation of a new length-based model of the dynamics of fish or crustacean stocks. We restrict attention to a single-species approach that is based entirely on scientific survey data.

The motivation for the study is to increase our ability to make reliable predictions of fish stock dynamics. As a prerequisite, the objective of our modelling is to understand the essence of the information on survey catchability and the vital rates of growth, mortality, and recruitment that is contained in data by validating models of differing complexity. If we can test for model complexity and obtain estimates of vital parameters with confidence limits, then our approach has a promising potential.

The validation of model complexity is done by testing statistical, hierarchical hypotheses. The basic hypothesis to be tested concerns the statistical distribution of the observed catch per unit of effort (CPUE) by length. Can a Poisson model for random encounters adequately describe the observations, or must we use an overdispersed distribution, such as the negative binomial (NB)? Choosing an adequate distribution is crucial because an inadequate distribution may seriously affect test results and parameter estimates. These problems will be pinpointed. Results of testing have not been reported in previous studies, where the stochastic variations in CPUE by length have been described by the normal (Sullivan 1992), the log-normal (Froysa et al. 2002; Fu and Quinn 2000), or the conditional multinomial (Froysa et al. 2002; Schnute and Fournier 1980; Smith et al. 1998) distributions. When a statistical distribution has been accepted, the next step in the hierarchical testing of hypotheses is to test if a comprehensive stock dynamics model can be accepted. If the comprehensive model is accepted, more simple submodels can be tested. To our knowledge, nobody has statistically tested model complexity of the stock dynamics model used.

Available models of length-based stock dynamics applying statistical methods are usually age–length structured. Froysa et al. (2002) and Schnute and Fournier (1980) combined standard, age-structured stock dynamics models with growth models and applied the derived models to length-based catch ob-

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servations, while Sullivan (1992) applied a purely length-based state–space model. Sullivan (1992) and Frøysa et al. (2002) approximated the discrete probabilities that fish either do not grow or grow into the neighbor length intervals for each length group. Other authors directly estimated the parameters of the von Bertalanffy growth equation (VBGE) assuming that mean length-at-age follows a specified distribution around a VBGE curve (Schnute and Fournier 1980; Fournier et al. 1998; Fu and Quinn 2000). These age–length structured approaches include both recruitment and temporal dynamics and are discrete in length and time. However, recruitment is assumed to take place instantaneously the same time each year, disregarding the fact that recruitment generally occurs continuously over time with an annually varying peak. Furthermore, the discretization implies some limitation in model assumptions. For instance, Sullivan (1992) and Frøysa et al. (2002) assumed that the probabilities of growing into neighboring length intervals were constant over time. Even if fish growth remains unchanged, this assumption is violated if the length-specific mortality varies over time. Smith et al. (1998) avoided the problems of discretization by using a continuous, statistically based spectrum model with individual variability in growth and length-dependent mortality. Their approach, however, assumed the stock to be in steady state and was therefore unable to consider temporal changes in mortality and recruitment.

There are two reasons why we developed a new approach to modelling the length-based fish stock dynamics. First, to produce a generic model platform we want to avoid possible bias of discretization (Xiao 2005) by formulating a time- and length-continuous model. Second, we want to include continuous recruitment, individual-based growth, and temporal changes of survey catchability because we want to test the importance of these processes. Such requirements are conveniently dealt within a time- and size-continuous approach (i.e., a size-spectrum model).

In the present paper, model complexity is tested by the likelihood ratio test. Regarding the continuous recruitment model, the timing of the recruitment peak and its variation is allowed to change by year and is estimated by the model. Individual growth is modelled using the VBGE assuming that each individual has its own von Bertalanffy asymptotic size (L_∞). Length-structured models for survey catchability and fishing and particularly natural mortality are also included. The estimability of the parameters is examined by Monte Carlo simulation. Only data from scientific surveys are applied, while fishery data are not included in the analysis. One reason for this is that testing whether a specified distribution adequately describes data requires that several independent observations are available following the same distribution in question. Such observations are only provided from surveys conducted within a short time range and selecting individual hauls randomly in an area. The use of survey data is further relevant when the quality of catch data is poor or when such data are not available. Finally, only length-based data are used, which is especially relevant when the age determination is uncertain. The present length-based model is applied to research survey data for Atlantic cod (*Gadus morhua*) in the eastern Baltic for which both problems apply (Reeves 2003). Survey-based but age-structured methods have also been considered by Cook (1997) and Beare et al. (2005).

Modelling the number density of a population

In the present model, the life history of an individual is determined by growth and mortality. Each individual is assumed to follow its own growth pattern, while the mortality depends on the size of the individual and the time. Recruitment is assumed to take place continuously in time. However, first we derive the number density in case of discrete recruitment. (Refer to the List of symbols for an explanation of all symbols used.)

Let R_0 denote a number of individuals recruited at the same time t_0 with the same size L_0. The fish growth is modelled using the VBGE. All individuals are assumed to have the same growth parameter k, while L_∞ varies individually following a common distribution with density u on (L_0, ∞). For an individual fish with a given L_∞, the length at time t is

$$(1)\qquad \begin{aligned} L(t, L_\infty) &= L(t, L_\infty|k, t_0, L_0) \\ &= L_\infty - (L_\infty - L_0)\exp[-k(t - t_0)] \end{aligned}$$

At time t the individuals that have size less than x are exactly the ones with an L_∞ belonging to the set

$$(2)\qquad \{L_\infty : L(t, L_\infty) \le x\} = [L_0, G(x)]$$

where

$$(3)\qquad G(x) = G(x|k, t_0, L_0) = \frac{x - L_0\exp[-k(t - t_0)]}{1 - \exp[-k(t - t_0)]}$$

Let $z(x, t)$ denote the size- and time-dependent total mortality. Then the number of survivors with size contained in the interval (L_0, x) at time t is given by

$$R_0 \int_{L_0}^{G(x)} \exp\left\{-\int_{t_0}^{t} z[L(s, L_\infty), s]\,\mathrm{d}s\right\} u(L_\infty)\,\mathrm{d}L_\infty$$

By differentiation with respect to x of this expression, we obtain the number density n based on a group of individuals recruited at the same time:

$$\begin{aligned} n(x, t) = R_0 \exp\left(-\int_{t_0}^{t} z\{L[s, G(x)], s\}\,\mathrm{d}s\right) \\ \times u[G(x)]G'(x) \end{aligned}$$

It should be kept in mind that both L and G depend on k, t_0, and L_0. To find the n based on a continuously recruited population, we simply add the corresponding number densities. Let $r(t)$ denote the recruitment rate. Then n at time t is

$$(4)\qquad \begin{aligned} n(x, t) = \int_{-\infty}^{t} r(t_0)\exp\left(-\int_{t_0}^{t} z\{L_{t_0}[s, G_{t_0}(x)], s\}\,\mathrm{d}s\right) \\ \times u[G_{t_0}(x)]G'_{t_0}(x)\,\mathrm{d}t_0 \end{aligned}$$

It may be noted that eq. 4 alternatively could have been derived directly from solutions $n(x, t, L_\infty)$ to the size-structured von Foerster equation (von Foerster 1959) for a given value of L_∞ and then mixing all these solutions with respect to the probability density $u(L_\infty)$. We shall refer to eq. 4 as a size-spectrum model.

Statistical model

Formulation

The ns from the previous section are now used to formulate a statistical model for catch data from hauls at random positions. The individual hauls are numbered by $i \in I$ and the time of the ith haul is denoted t_i. The set of sampling times is given by $T = \{t_i : i \in I\}$. It is assumed that for each $t \in T$ the set $\{i \in I : t_i = t\}$ has at least two elements (i.e., for each sampling time, we have at least two hauls).

Within each haul, individual fish are measured with an arbitrary accuracy and associated with a corresponding length group C_j. Data can be summarized by a matrix N_{ij} of counts for the jth length group at the ith haul.

We consider a simple statistical model with a corresponding hierarchy of hypotheses ($H_0 \supset H_1 \supset H_2 \supset H_3$).

H_0

In our main statistical model, N_{ij} are assumed to have an independent, NB distribution with identical parameters within each sampling time ($t \in T$) and length group (j) (i.e., the random variables $\{N_{ij} : t_i = t\}$ are identically distributed with mean $\mu_{t,j}$ and variance $\sigma^2_{t,j}$ ($\sigma^2_{t,j} > \mu_{t,j}$)). To be able to estimate parameters in this model, we need at least two hauls for each sampling time.

The likelihood function is given by

$$L[(\mu_{t,j}),(\sigma^2_{t,j})] = \prod_i \prod_j \frac{\Gamma(N_{ij} + v_{t_i,j})}{\Gamma(v_{t_i,j})\Gamma(N_{ij}+1)} \times \pi_{t_i,j}^{v_{t_i,j}}(1-\pi_{t_i,j})^{N_{ij}}$$

in terms of the density function of the NB distribution with probability parameter $\pi_{t_i,j} = \mu_{t_i,j}/\sigma^2_{t_i,j}$ and size parameter $v_{t_i,j} = \mu^2_{t_i,j}/(\sigma^2_{t_i,j} - \mu_{t_i,j})$. Note that for a given sampling time t, the maximum likelihood estimate $\hat{\mu}_{t,j}$ is just the group average, while $\hat{\sigma}^2_{t,j}$ can not be written on closed form.

H_1

To reduce the number of parameters in the main model, we state the variance structure hypothesis:

$$V(N_{i,j}) = \sigma^2_{t_i,j} = a_{t_i}\mu_{t_i,j}^{b_{t_i}} + \mu_{t_i,j} \tag{5}$$

This variance structure is mainly proposed from empirical investigations (even though we can give a mechanistic argumentation in the case of $b_{t_i} = 2$, which is out of the scope of this paper). Note that the additional $\mu_{t_i,j}$ term ensures that $\sigma^2_{t_i,j} > \mu_{t_i,j}$, which is required by the NB distribution.

H_2

The size-spectrum model with time-dependent catchability is simply a mean value hypothesis in the previous models obtained by assuming the variance structure (eq. 5) and expressing the expected CPUE in terms of catchability and number densities:

$$E(N_{i,j}) = \mu_{t_i,j} = \int_{C_j} q_\theta(x,t_i) n_\theta(x,t_i)\,\mathrm{d}x \tag{6}$$

The relevance of letting the catchability be time-dependent will be justified.

H_3

Finally we may consider the time-independent catchability model by assuming that $q(x,t) = q(x)$ in H_2:

$$\mu_{t_i,j} = \int_{C_j} q_\theta(x) n_\theta(x,t_i)\,\mathrm{d}x$$

Setting up a hierarchy of hypotheses like this has several benefits. First of all it enables successive statistical tests to validate the spectra models. But more importantly it helps us to localize model problems. For example, the model H_2 includes three different assumptions regarding the statistical distribution, a variance structure, and a mean value structure. If the H_2 hypothesis has problems fitting the data, it will be possible to find out which of the three assumptions are critical by considering successive likelihood ratios.

To validate the main model (H_0) we use the randomization technique described in Appendix A because the random variables N_{ij} have a discrete distribution (and thus, transforming with its distribution function, does not produce a uniform distribution). To test the hypotheses H_1,H_2, and H_3, we use likelihood ratio testing for composite hypotheses (Rao 1965).

Parametrization

The catchability function is chosen as a symmetric sigmoid curve multiplied by a fishing power p_t.

$$q_\theta(x,t) = \frac{p_t}{1 + \exp[-\alpha_t(x - L^{q}_{50})]} \tag{7}$$

Both p_t and α_t depend on the time t of the survey. α_t thus describes changes in the selection pattern over time, while p_t models changes in the overall catch efficiency in the survey.

The mortality z is split into two components: the natural mortality and the fishing mortality:

$$z(x,t) = M_0 + f(x,t)$$

where M_0 is an assumed unknown constant, and f is assumed to split into the product of a piecewise constant function of time and a sigmoid function of size

$$f(x,t) = \frac{1}{1 + \exp[-\beta(x - L^{f}_{50})]} \sum_{i=1}^{n} F_\infty^{(i)} 1_{(\tau_{i-1}<t<\tau_i)}$$

For the distribution of $L_\infty(u)$ we use a normal distribution with mean μ_{L_∞} and standard deviation σ_{L_∞}. When there are almost no observed fish larger than $\sim 1/2\mu_{L_\infty}$ (actually 50 cm in our case), it is impossible to estimate μ_{L_∞} and k simultaneously. Therefore, it is assumed that μ_{L_∞} is known and a value from Bagge et al. (1994) is used.

New individuals are recruited to the size of L_0 continuously in time. It is assumed that the recruitment period for a year class is normally distributed. Hence the recruitment rate is a linear combination of normal components:

$$r(t) = \sum_{y \in Y} R_y \phi_{\mu_y^{\mathrm{rec}},\sigma_y^{\mathrm{rec}}}(t) \tag{8}$$

where $\phi_{\mu,\sigma}$ is the normal density with mean μ and standard deviation σ. The mean recruitment time for cohort y is parameterized as a year y plus a date Δt_y (i.e., $\mu_y = y + \Delta t_y$).

We use $L_0 = 1$ cm and $Y = \{1997, \ldots, 2003\}$ in the present case.

The parameters of the statistical model H_2 are summarized in the vector $\boldsymbol{\theta}$:

$$\boldsymbol{\theta} = \Big(R_{1997}, R_{1998}, R_{1999}, R^{*}_{2000} = 1, R_{2001}, R_{2002}, R_{2003}, \Delta t_{1997}, \ldots, \Delta t_{2003}, \sigma^{\text{recr}}_{1997}, \ldots, \sigma^{\text{recr}}_{2003}, p^{\text{survey}}_{t}, L^{\text{survey}}_{50}, \alpha^{\text{survey}}_{t}, k, \mu^{*}_{L_\infty} = 135, \sigma_{L_\infty}, L^{\text{fishery}}_{50}, \beta^{\text{fishery}}, F^{(<2001)}_{\infty}, F^{(2001-2002)}_{\infty}, F^{(2002-2003)}_{\infty}, F^{(>2003)}_{\infty}, M_0, a^{\text{variance structure}}_{t}, b^{\text{variance structure}}_{t}\Big) \tag{9}$$

An asterisk (*) indicates that the parameter is fixed.

Identifiability

Some care is needed to avoid that the spectra models H_2 and H_3 get overparameterized. Since the statistical models are determined by the mean values (eq. 6), we need to dispel all obvious parameter bands appearing here. First of all, by inserting eq. 4 in eq. 6, notice the band between the parameter vector (p_t) and the vector of recruitment sizes (R_y); if we multiply and divide the two vectors, respectively, with the same constant, the model is unchanged. This is taken care of by fixing one of the recruitments to 1 (e.g., $R_{2000} = 1$). With this convention, it is possible to estimate the parameters in both statistical models based on the parametrization given in the previous section. This claim has been verified by re-estimating known parameters in simulated data sets.

However these Monte Carlo experiments showed that a large number of the parameters in the model were highly correlated, indicating the need for a reparametrization. Especially high correlations occurred between a and b from the variance structure and among (p_t) from the catchability. The transformation $(\tilde{a}, \tilde{b}) = (\log a + b\ :\ \overline{\log \mu}, b)$ made $\tilde{a}$ and $\tilde{b}$ almost uncorrelated. Furthermore, it appeared that the variables $\log p_{t_1}, \log p_{t_2} - \log p_{t_1}, \log p_{t_3} - \log p_{t_2}$, etc. were much less correlated than the vector $(\log p_t)$. Also the choice of reference year class had a major impact on the range of correlations between the parameter estimates.

With the new parametrization, a Monte Carlo re-estimation experiment was carried out. All parameter estimates were plotted in pairs to determine deviations from the asymptotic normal distribution. The plots showed regular ellipses, indicating that the normal approximation applies.

Model predictions

Once we have obtained the estimate $\hat{\boldsymbol{\theta}}$, we can compute model predictions of, for example, the relative biomass and length distribution of the commercial catches. Assuming isometric growth (i.e. $W = q_0 L^3$) for some condition factor q_0, the total biomass in the system at time t is given by

$$B(t) = q_0 \int_{L_0}^{\infty} x^3 n(x, t)\, \mathrm{d}x \tag{10}$$

Recall that since $R_{2000} = 1$ is fixed, $n(x, t)$ is only known up to a multiplicative constant. Therefore, eq. 10 can only be used to predict the relative biomass in the system, and for that purpose q_0 is not needed. We may compute the number density of the fishery catch during the time period I by the formula

$$c_I(x) = \int_I f(x, t) n(x, t)\, \mathrm{d}t \tag{11}$$

This formula makes it possible to compare the catches for a given length group between different time periods.

To compare results with those from age-based models, it is useful to convert length-specific mortalities to age-specific mortalities. For a given cohort, the overall mortality at time t is given by $z_{\text{cohort}}(t) = -N'(t)/N(t)$, where $N(t)$ is the total number of individuals in the cohort at time t. Hence

$$z_{\text{cohort}}(t) = \frac{\int_{L_0}^{\infty} z(x, t) n_{\text{cohort}}(x, t)\, \mathrm{d}x}{\int_{L_0}^{\infty} n_{\text{cohort}}(x, t)\, \mathrm{d}x} \tag{12}$$

This equation also applies when replacing z by m or f.

Data

Our data consist of cod catches from 299 selected hauls obtained from the Baltic International Trawl Survey. Only positions inside the International Council for the Exploration of the Sea (ICES) division 25 are considered. All the hauls are taken with TVL-trawl by the Danish vessel *DANA*. The duration of a haul is ~ 30 min.

The survey is performed twice a year — the spring survey, which takes place around 1 March, and the autumn survey, which takes place around 1 November. The actual haul times are distributed over a 1-month interval around these dates, and we associate an average date with each survey — the so-called sampling time.

A brief overview of the data is given in Table 1. The length of each fish has been measured to an accuracy of 1 cm and a length range from 5 to 60 cm is considered. We define the mean CPUE for a given 1 cm length group as the average number of fish caught at a given time for that given length group in a haul. The mean CPUEs per length group are illustrated (Fig. 1), and von Bertalanffy growth curves are also shown (with parameters given in the caption) in order to follow the cohorts through time. The positions of the peaks in the length distributions are reasonably well described by the growth curves. The growth

Fig. 1. Catch per unit of effort (CPUE) per 1 cm length group at the nine sampling times and Bertalanffy curves with initial size $L_0 = 1$ cm at 1 August. Each Bertalanffy curve is marked with the two-digit year classes from 1995 to 2003. Except for the initial time t_0, all curves have the same parameters $k = 0.12$ year^{-1} and $L_\infty = 135$ cm.

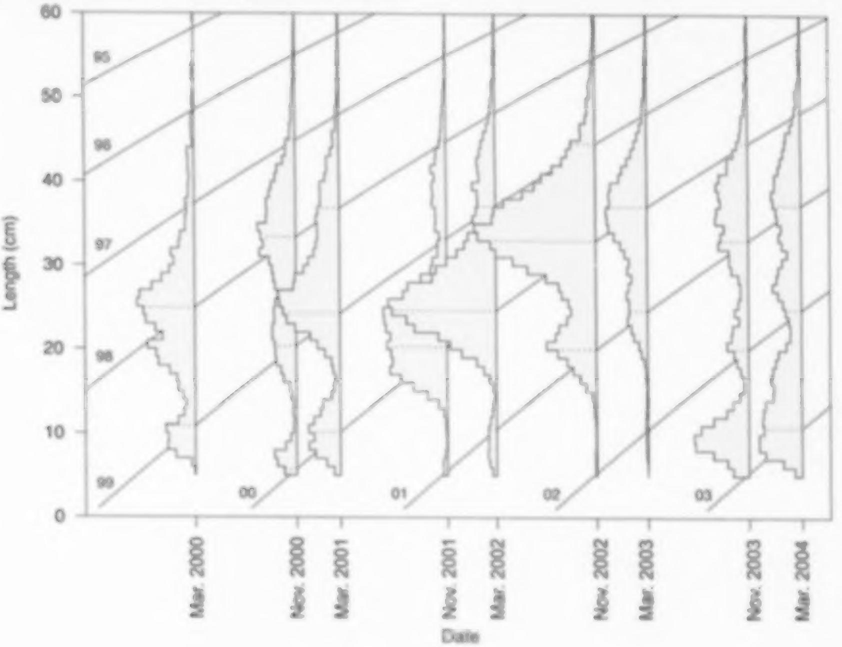


Table 1. Number of hauls and fish caught by survey.

Survey	No. of hauls	No. of fish caught
Mar. 2000	8	1 920
Nov. 2000	29	6 300
Mar. 2001	50	13 658
Nov. 2001	33	8 610
Mar. 2002	41	14 733
Nov. 2002	35	16 796
Mar. 2003	41	7 467
Nov. 2003	24	5 870
Mar. 2004	38	10 857

curves also indicate the extent it is possible to estimate recruitment. It is impossible to estimate the 95 and 96 year classes, as virtually no fish older than 3 years are caught. The year class with the clearest data signal is the 2000 year class; hence it is natural to use the 2000 year class as a reference. All other year classes will be estimated.

Results

Validating the main statistical model

The model H_0 includes both a distributional assumption and an assumption about independence. These are considered separately. For each of the nine surveys and 55 cm length groups, the maximum likelihood estimates (MLEs) $\hat{\mu}_{t_i}$ and $\hat{\sigma}_{t_i}^2$ have been obtained. By transforming with the estimated distribution function — and randomizing as described in Appendix A — we obtained 299 × 55 residuals (U_{ij}), which should follow a uniform distribution on the unit interval. A quantile-quantile (Q-Q) plot indicates that this holds true (Fig. 2*a*). The same residuals (U_{ij}) were also plotted against μ_{t_i} (Fig. 2*b*), showing no systematic patterns.

To demonstrate the importance of choosing a distribution with over-dispersion, the same plots were made with the NB distribution replaced by the Poisson distribution (Figs. 2*c* and 2*d*). The Poisson distribution obviously did not meet the criterion of uniformity.

The model H_0 assumes independence between length groups. To validate this assumption, the empirical correlations between length groups were examined, and it appeared that strong correlations existed between neighboring length groups.

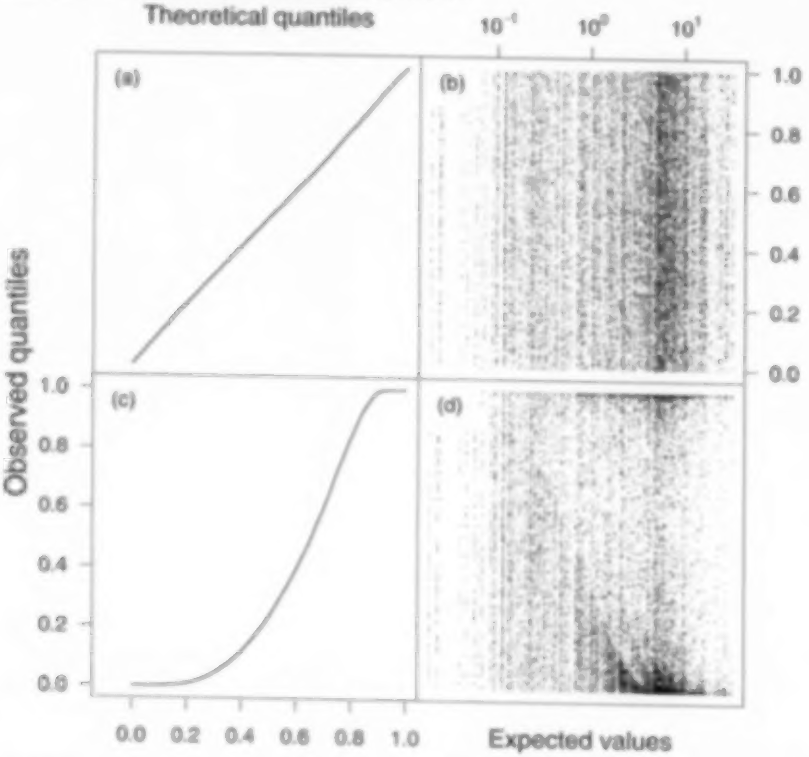
In the light of the length group dependencies, it did not make sense to perform a formal Kolmogorov–Smirnov test on the randomized residuals ($U_{i,j}$) to test whether these residuals followed a uniform distribution. Instead we chose to partition the residuals into corresponding 1 cm length groups (i.e., considering U_{ij} for fixed j) and performed the statistical test for each of the length groups in order to test the distributional assumption. Indeed, this lead to acceptance for every group.

We will ignore the length group dependencies throughout this study.

Examining the variance structure

To reduce the number of parameters in the main model (H_0), the variance structure proposed in H_1 is suggested, which al-

Fig. 2. (*a*) Q-Q plot for the negative binomial (NB) distribution. The observed randomized quantiles are plotted against the theoretical quantiles. (*b*) The observed randomized quantiles for the NB distribution as a function of the estimated mean value parameter. (*c*) Q-Q plot for the randomized quantiles based on the Poisson distribution. (*d*) The observed randomized quantiles for the Poisson distribution as a function of the estimated mean value parameter in the Poisson distribution.



most eliminates half of the parameters. The reasonability of this hypothesis is justified (Fig. 3), showing nine independent analyses — one for each sampling time. The parameter estimates ($\hat{\mu}_{t,j}$ and $\hat{\sigma}^2_{t,j}$) from the full statistical model (H_0) are plotted for each sampling time together with the curve $\sigma^2 = \hat{a}_t \mu^{\hat{b}_t} + \mu$, where $\hat{a}_t$ and $\hat{b}_t$ are the MLEs from the variance structure model (H_1) at time t.

Despite the convincing fits on Fig. 3, the likelihood ratio test of H_1 against H_0 is rejected. It turns out that the points above the curves generally correspond to fish smaller than 20 cm, while points below the curves correspond to fish larger than 20 cm. This motivates an extension H_1' of H_1 with two variance structures for each survey — one for fish smaller than and one for fish larger than 20 cm. It is later shown that H_1' is accepted under H_0 (Table 2).

Spectrum model inference

Assuming the hypothesis H_1', we now consider the size-spectrum model (H_2) with time-dependent catchability. It was assumed that the mean date and the standard deviation of the recruitment process was the same for all year classes earlier than the first sampling time, i.e.:

$$\begin{aligned} \sigma^{\text{recr}}_{1997} &= \sigma^{\text{recr}}_{1998} = \sigma^{\text{recr}}_{1999} \\ \Delta t_{1997} &= \Delta t_{1998} = \Delta t_{1999} \end{aligned} \tag{13}$$

The MLE $\hat{\boldsymbol{\theta}}$ for $\boldsymbol{\theta}$ (eq. 9) was obtained, and the Hessian matrix was checked to be positive definite. Based on $\hat{\boldsymbol{\theta}}$, the expected CPUEs $\mu_{t_i,j}$ were computed and compared with the observed mean CPUEs (Fig. 4). We conclude that the model H_2 describes the CPUEs well. Moreover, H_2 was accepted by a formal likelihood ratio test (Table 2).

Assuming constant catchability (i.e., time-independent α_t and p_t) over time, we estimated parameters based on H_3 and obtained a plot equivalent to Fig. 4, which showed that it was impossible for the reduced model to explain the increasing CPUE for the 2000 cohort during year 2002.

To overcome this problem, we also considered a compromise (H_3') between H_2 and H_3 with time-independent α_t and time-dependent p_t. The visual fit was improved compared with H_3. However both H_3 and H_3' were rejected by the likelihood ratio test (Table 2).

It became apparent that no simple reduction of H_2 was possible (Fig. 5). To arrive at a final model, the estimates from H_2 were inspected, and the ones that did not differ significantly were collected to form a final hypothesis (H_2'):

$$\begin{aligned} &p_4 = p_5 = p_6 \\ &\alpha_1 = \alpha_2 = \alpha_4 = \alpha_5, \quad \alpha_3 = \alpha_6 = \alpha_7, \quad \alpha_8 = \alpha_9 = 0 \\ &\sigma^{\text{recr}}_{1997} = \sigma^{\text{recr}}_{1998} = \sigma^{\text{recr}}_{1999}, \quad \sigma^{\text{recr}}_{2000} = \sigma^{\text{recr}}_{2001} = \sigma^{\text{recr}}_{2002} \\ &\Delta t_{1997} = \Delta t_{1998} = \Delta t_{1999} = \Delta t_{2000} \end{aligned} \tag{14}$$

Fig. 3. Maximum likelihood estimates (MLEs; circles) $\hat{\sigma}_i^2$ vs $\hat{\mu}_i$ from the main model (H_0). Solid lines indicate the function $\sigma^2 = \hat{a}_t\mu^{\hat{b}_t} + \mu$, where $\hat{a}_t$ and $\hat{b}_t$ are the MLEs from the variance structure model (H_1) at time t.

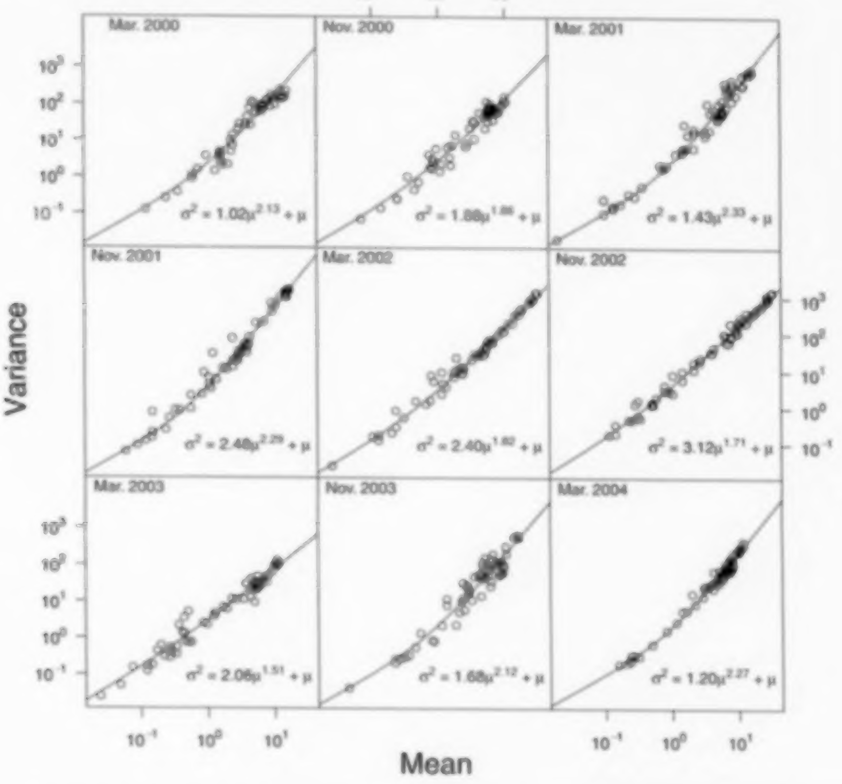


Table 2. (*i*) Successive asymptotic likelihood ratio tests. (*ii*) Sequential tests under H_2 of H_3 (time-independent catchability) and H_3' (time-independent α_t in catchability).

		$-\log L$	$-2\log Q$	No. of parameters	df	p
(*i*)	H_0	34 320.0	—	990	—	—
	H_1'	34 565.3	490.7	531	459	0.15
	H_2	34 779.6	428.6	80	451	0.77
(*ii*)	H_3	35 040.5	521.7	64	16	< 0.01
	H_3'	34 823.9	88.6	72	8	< 0.01
	H_2'	34 789.2	19.3	68	12	0.08

The likelihood ratio test of H_2' against H_2 was accepted (Table 2). Also the likelihood ratio test of H_2' against H_0 supported this conclusion with $p = 0.35$. To validate the applied χ^2 approximation, a simulation study was carried out: 100 data sets were randomly generated from H_2', and the the likelihood ratio test of H_2' under H_0 was computed. The simulated distribution agreed perfectly with the theoretical χ^2 distribution with 922 (990 − 68) degrees of freedom.

The final model H_2' had 68 parameters, of which 36 described the variance structure and 32 described the expected CPUEs. A plot of the expected CPUEs did not produce any visible changes from Fig. 4.

The highest absolute parameter correlations in the reduced model were found to be 0.93. However, those correlations involving the mean value parameters were all below 0.90.

The parameters with the highest coefficient of variation (CV) were $\mathrm{CV}(\widehat{M}_0) = 0.66$, $\mathrm{CV}(\widehat{\beta}) = 0.33$, and $\mathrm{CV}(\widehat{\log R_0}) = 0.36$. Almost all other parameters had $\mathrm{CV} < 0.20$.

To test the significance of continuous recruitment versus instantaneous recruitment, the confidence intervals of σ_y^{recr}, $y = 1997, \ldots, 2003$ were considered. It appeared that none of these included 0. Also, the standard deviation on L_∞ was significantly greater than 0, showing that a model assuming identical growth trajectories for all individuals would be rejected even if individual variability in the spawning time was included.

Spectra model predictions

From the parameter estimates based on H_2, different kinds of model characteristics were computed — namely the estimated biomass, mortality, and recruitment. Furthermore, the predicted commercial landings were compared with the observed ones.

The biomass relative to year 2002 (i.e., $B(t)/B(2002)$, where $B(t)$ is computed by eq. 10) is shown (Fig. 6*c*). The increasing trend during 2002–2003 was mainly caused by the strong 2000 year class (Fig. 6*b*).

Fig. 4. Observed catch per unit of effort (CPUE) and expected CPUE per 1 cm length group at each sampling time obtained from model H_2'.

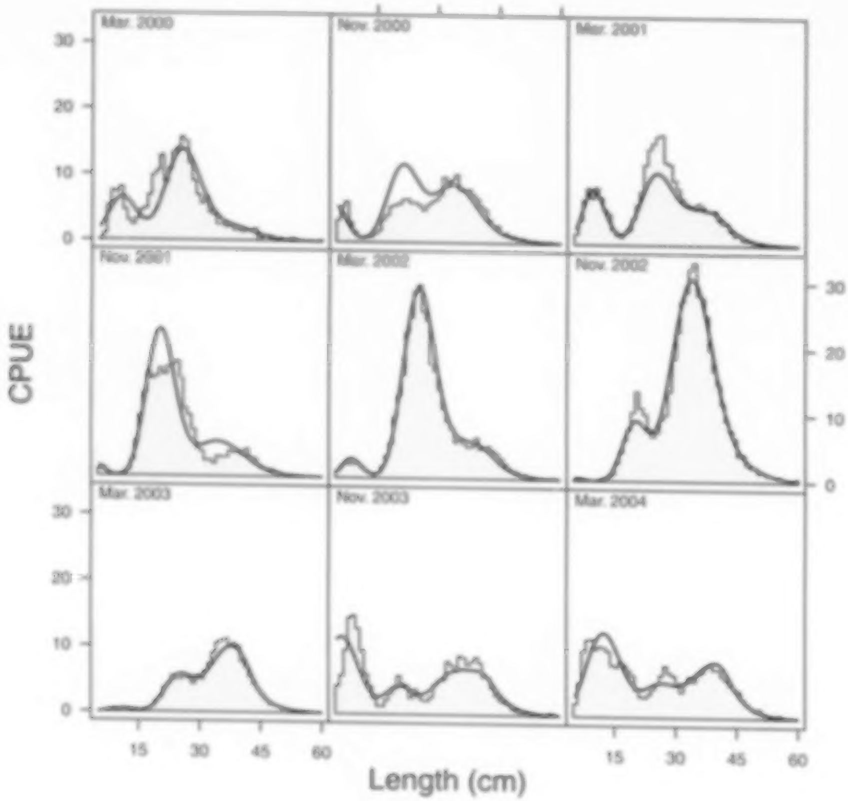


Fig. 5. Hypothesis hierarchy. H_0, main statistical model without mean and variance assumptions; H_1, variance structure model; H_1', extended variance structure model; H_2, size-spectrum model with multiplicative time-dependent catchability; H_3, time-constant catchability; H_3', time variability in catchability caused by fishing power alone; H_2', final accepted hypothesis obtained by collecting parameters in H_2.

$$\begin{tikzcd}
H_0 \arrow[r] \arrow[dr] & H_1 & & H_3 \\
& H_1' \arrow[r] & H_2 \arrow[ur] \arrow[r] \arrow[dr] & H_3' \\
& & & H_2'
\end{tikzcd}$$

No information on the commercial landings has been utilized for model estimation, but catch compositions are available from 2000 until ultimo 2003. The predicted length probability distributions of the yearly commercial landings in that period were computed by eq. 11 and compared with the observed distributions (Fig. 6*d*). The predictions fit the observations quite well for all years. However, when considering the absolute commercial landings over the same period, there is a clear decreasing trend that is not replicated by the model (not shown).

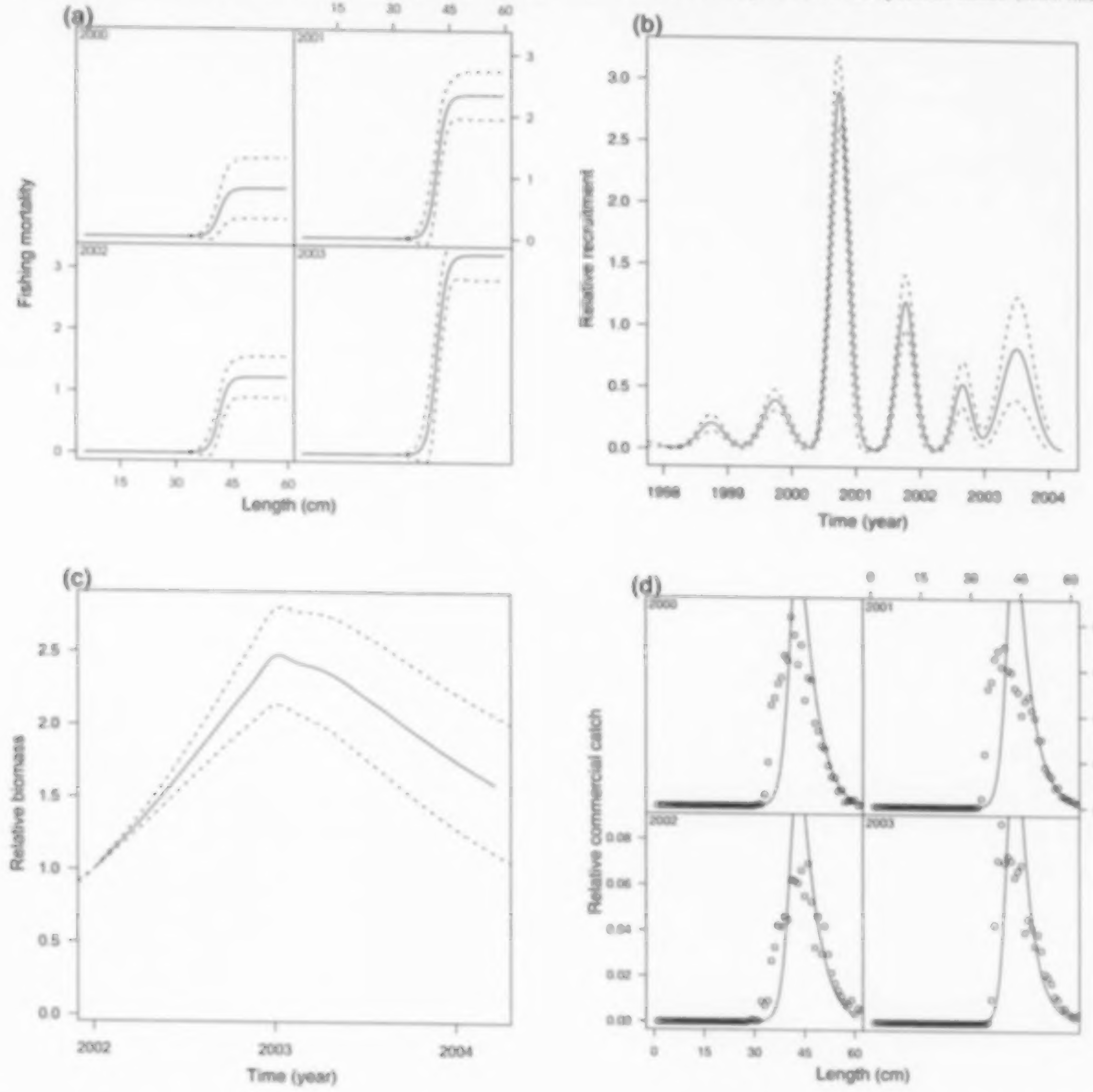
The age-specific fishing mortalities were computed (Table 3) based on eq. 12. These mortalities were slightly lower than the size-specific mortalities (Fig. 6*a*). The reason for this is that only the fraction consisting of the fastest growing individuals of an age group is exposed to the high size-specific mortalities. This phenomenon is maintained by the increasing size dispersion within a cohort implied by the underlying stochastic growth model.

Another consequence of the extreme size-selective mortality is the emergent property that old individuals grow very slowly. This is illustrated by showing the mean of the single cohorts as a function of time (Fig. 7). From this illustration we can conclude that for the typical length distribution of fish within a given survey — which consists of three peaks — the first and second peaks consist primarily of the 0-group and 1-group, respectively, while the third peak consists of all other age groups.

Discussion

This paper validates a new length-structured model of stock dynamics by testing hierarchically classified hypotheses. Hence,

Fig. 6. (*a*) Estimated fishery mortality (solid lines) and 95% confidence limits (broken lines) by fish size. (*b*) Estimated recruitment R_i by year and 95% confidence limits. (*c*) Estimated relative biomass and 95% confidence limits. (*d*) Observed relative length distributions for the commercial catches (circles) and predicted relative length distributions for the fishery based on the spectrum model (solid line).



the approach makes it possible to investigate model complexity, a necessary prerequisite for determining stock dynamics, which is particularly crucial for complex, nonlinear models. Only survey data have been used. Testing hypotheses requires that the applied statistical distribution adequately describes the variation of the observations, and the correspondence between the observations and the distribution should be investigated either graphically or by a formal test. This has been done for observations in the case study here, where the hypothesis of an NB distribution with a specified variance–mean structure was accepted. Testing the significance of a statistical distribution is only possible if several independent, identically distributed observations are available and analysed without prior aggregation as done in the present approach. The NB distribution with an unspecified mean and with the specified variance structure was subsequently used as a general model against which submodels of interest have been tested. The present size-spectrum model is such a submodel specifying the mean of the NB distribution. The spectrum model has been tested against the basic NB model and was accepted. To our knowledge, no previous stock dynamics or assessment approach has formally tested the significance of the model applied.

Fig. 7. Estimated mean of the individual cohorts (solid lines) and von Bertalanffy curves from Fig. 1 (broken lines).

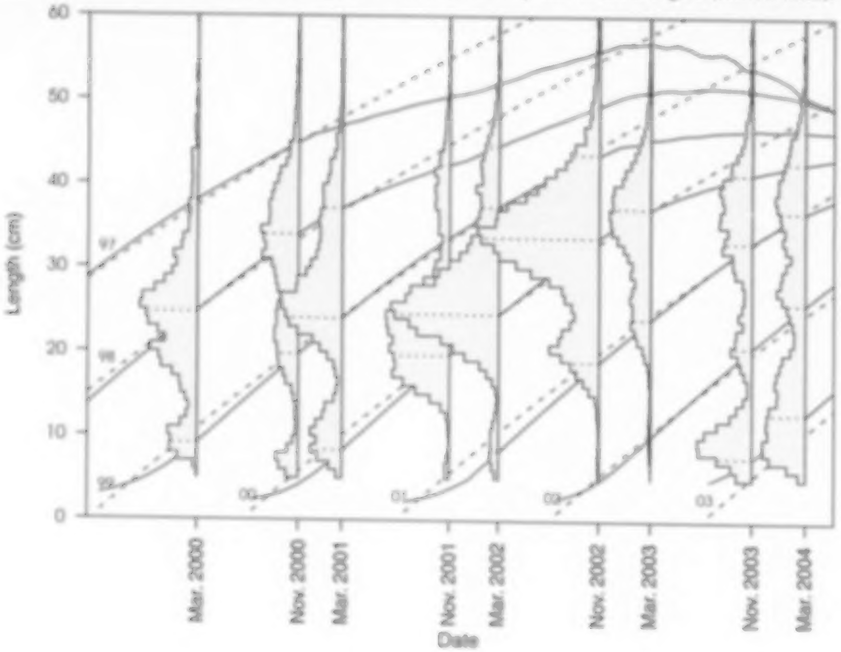


Table 3. Age-specific fishing mortality.

Date	Age (years) 0	1	2	3	4	5	6
Mar. 2000	0	0	0.21	0.62	0.75	—	—
Nov. 2000	0	0	0.08	0.53	0.72	0.77	—
Mar. 2001	0	0	0.51	1.75	2.17	2.28	—
Nov. 2001	0	0	0.18	1.23	1.89	2.16	2.25
Mar. 2002	0	0	0.28	0.81	1.04	1.14	1.18
Nov. 2002	0	0	0.09	0.75	1.04	1.11	1.15
Mar. 2003	0	0	0.67	2.22	2.78	2.90	2.98
Nov. 2003	0	0	0.18	1.51	2.23	2.54	2.59
Mar. 2004	0	0	0.60	1.79	2.19	2.34	2.33

The stock dynamics model developed combines the characteristics of continuous recruitment in time, individual based growth, and continuous, size-dependent mortality rates. As recruitment is assumed to take place continuously, it is possible to test the simpler model of instantaneous recruitment. The model with instantaneous recruitment (with estimation of the optimum time of recruitment) resulted in problems with the interpretation of growth parameters, as the probability of obtaining unrealistic small L_∞ (e.g., < 20 cm) was non-negligible. This problem arose because the standard deviation of L_∞ (σ_{L_∞}) would compensate for the lack of spawning variation, resulting in too large estimates of σ_{L_∞}. These problems were the main reason for the statistical rejection of the spectrum model with instantaneous recruitment. In contrast, the model assuming continuous recruitment did not encounter any of these problems. First, the continuous recruitment model was accepted, and secondly, the distribution of L_∞ can be described by the normal distribution, with negligible possibility of negative values of L_∞ and with a reasonable estimate of k. An additional advantage of modelling and estimating recruitment continuously over time by the annual timing of the peak and its temporal variation is the possibility of investigating and studying recruitment processes.

For the model H_5', it was possible to estimate a constant natural mortality, M_0. The estimability of M_0 is in agreement with Fu and Quinn (2000), suggesting that (in another length-based model for *Pandalus borealis*) constant M_0 can be estimated together with a survey catchability varying over time. Assuming, however, that $m(x,t)$ is constant for all fish sizes is of course incorrect, as $m(x,t)$ increases for the smaller fish (ICES 2005*a*). We therefore formulated an alternative, more biologically realistic model by expressing $m(x,t)$ as a size-dependent function, $m(x) = 23\exp(-x+1) + M_\infty$, which is equal to 23 for fish of length 1 cm, decreases to M_∞ when the fish length increases, and is close to M_∞ for x larger than 5 cm. The mortality rate of 23 corresponds to the value used by Bradford (1992) as late cod larvae daily mortality of 0.063. For this model, M_∞ was estimated to 0.16, which is close to and not significantly different from 0.18 previously estimated. The estimates of biomass, recruitment, and fishing mortality are likewise very similar for the two $m(x,t)$ assumptions. Neither did reducing the mortality rate of larval cod by 50% change the results. This suggests that natural mortality can be assumed constant for all sizes when estimating relative biomass, recruitment, and fishing mortality in the size-structured stock dynamics model.

The suggested model considers the individual growth of each fish. The assumption of individual growth patterns was formulated assuming that each fish has its own L_∞ and that the individual values originate from a normal distribution with a mean of 135 cm and a variance to be estimated. The estimated standard deviation of L_∞ is significantly larger than zero, indicating that the individual growth model is a major improvement compared with a growth model where all fish have the same growth. Individual variability could also be associated with k instead of L_∞, but results of Swain et al. (2003) suggest that for Atlantic cod the model implemented here fits better than the model with varying k.

The model is continuous in time and size, which has the advantage that the stock dynamics model is formulated independently of any discretization. Furthermore, observations can be used as a basis for estimation irrespective of the timing, which makes it possible to include additional catch or survey information collected at other times of the year.

The NB distribution was accepted adequately to describe data and was applied further in the calculations. To illustrate consequences of applying a wrong distribution, the Poisson distribution was applied, for which we know that the variance will be underestimated. The MLEs were calculated and the tests of H_2 and H_3 were carried out. The result was (not surprisingly) that both tests were rejected wrongly, indicating that the spectrum model does not adequately describe stock dynamics. For the H_2 model, the MLEs were significantly different from those obtained using the NB distribution.

High correlations were encountered between the number of fish caught per haul in adjacent length groups. Therefore, a multivariate NB distribution should have been used. Unfortunately, such a distribution does not exist. Intuitively, the high correlations should reduce the information in the data, resulting in more uncertain estimates. If the model was able to account for the correlations, we would expect higher test probabilities in general. This could potentially cause simpler model structures to be accepted.

The biomass and mortality estimates of the first 2 years of data are based primarily on assumptions on recruitment, its temporal distribution, and mortality rates for the years prior to the first data year. However, since the stock estimates for the first 2 years are sensitive to the assumptions made, these estimates are more uncertain than those of the following years, an uncertainty that is not reflected in the confidence limits shown. For cases with several years included, this is not so much a problem as it is for the present case, where only few years are included. It is actually surprising that the analysis can be performed based on data for only 5 years.

Estimated fishing mortality for fish larger than 45 cm and fish older than 3 years is very high (F ranges from 1 to 4) compared with the values of ~ 1 estimated by ICES (2005*b*). However, very high mortality rates are supported by the fact that only very few fish larger than 50 cm were caught in the surveys in 2000–2004. To assure that large fish are absent, mortality rates higher than 1 are required. The very high fishing mortality for fish larger than 45 cm, combined with a size selection close to knife-edge selection, results in a mature stock consisting mainly of slow-growing individuals, which have not yet reached a size of about 45 cm. This was indicated by showing that the mean length at age does not increase for fish older than 4 years. It is an open question whether this has led to long-term genetic stock changes.

In conclusion, the present model applied to size-structured scientific survey data is a promising tool to describe and critically examine stock dynamics of a stock for which age determination is uncertain and the quality of catch data is poor. Model complexity can be investigated by testing statistical hypotheses, where different spectra models can be tested thoroughly against a set of probability density distributions describing CPUE by length and haul for each survey. A spectrum model was statistically accepted for which natural mortality and fishing mortality rates, relative biomass and recruitment, and growth were estimated. It is remarkable that the approach reasonably reproduces the relative length distribution of the commercial landings without using these data. The model estimates of fishing mortality could potentially be improved by including commercial catch data by length. This may further enable the estimation of time-varying natural mortality rates.

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List of symbols

x	General notation for size
t	General notation for time
k	von Bertalanffy growth parameter
L_0	Recruitment size
L_∞	von Bertalanffy asymptotic size
$L(x, L_\infty)$	von Bertalanffy growth trajectory
$u(L_\infty)$	Density function describing the probability that an individual is assigned a given L_∞ at the time of recruitment
μ_{L_∞}	Mean value of L_∞
σ_{L_∞}	Standard deviation of L_∞
$z(x, t)$	Total mortality as function of size and time
$m(x, t)$	Natural mortality as function of size and time
M_0	Parameter in natural mortality
$f(x, t)$	Fishing mortality as function of size and time
F_∞	Parameter vector in fishing mortality
β	Parameter in fishing mortality
L_{50}^f	Parameter in fishing mortality
$\boldsymbol{\tau}$	Vector determining the piecewise constant levels in fishing mortality as a function of time
$r(t)$	Recruitment rate with the property that $r(t)\,\mathrm{d}t$ is the approximate number of individuals recruited to the minimum size L_0 during the time interval $(t, t + \mathrm{d}t)$
$n(x, t)$	Number density function with the property that the number of individuals with size in (x_1, x_2) at time t is given by $\int_{x_1}^{x_2} n(x, t)\,\mathrm{d}x$
$\boldsymbol{\theta}$	Vector containing all model parameters in a given model. Used as subscript (e.g., $n_{\boldsymbol{\theta}}(x, t)$) to indicate that the function $n(x, t)$ contains unknown parameters
I	Set of haul indices
T	Set of sampling times
Y	Set of recruitment year classes
N_{ij}	Matrix of observed number of fish for haul index $i \in I$ and size group $j \in J$
$\mu_{t,j}$	Expected number of fish in length group j in a haul taken at survey time $t \in T$
$\sigma_{t,j}^2$	Variance of the number of fish in length group j in a haul taken at survey time $t \in T$
a_t	Variance structure parameters indexed by survey time $t \in T$
b_t	Variance structure parameters indexed by survey time $t \in T$
R_y	Total recruitment for year class y
μ_y^{recr}	Mean recruitment time for year class y
Δt_y	Date of the mean recruitment time for year class y (i.e., $\Delta t_y = \mu_y^{recr} - y$)
σ_y^{recr}	Standard deviation of the recruitment rate for year class y
$q(x, t)$	Catchability function
p_t	Catchability parameter for $t \in T$
α_t	Catchability parameter for $t \in T$

Appendix A.

Randomization

Let N be a discrete random variable on $\mathbb{N}_0$ with distribution function F and let the conditional distribution $U|N = n$ be uniform on the interval $[F(n-1), F(n)]$. Then the distribution of U is uniform on $[0,1]$.

To prove this, let g be the density of U. The conditional density of $U|N = n$ is given by

$$g(u|n) = \frac{1}{P(N = n)} 1_{[u \in [F(n-1), F(n)]]}$$

Hence the unconditional density is

$$\begin{aligned} g(u) &= \sum_{n=0}^{\infty} g(u|n) P(N = n) \\ &= \sum_{n=0}^{\infty} 1_{[u \in [F(n-1), F(n)]]} \\ &= 1 \end{aligned}$$

for any $u \in [0,1]$.

Thus to test whether N has distribution function F, we should simulate a random variable U with a uniform distribution on $[F(N-1), F(N)]$ and then test whether U is uniform on $[0,1]$.

Computational methods

All computations have been carried out using R (R Development Core Team 2005). An open source R package has been developed for the purpose (available by contacting the authors). The package calls external C++ code, which takes advantage of the free package CppAD (Bell 2005) to evaluate analytical first- and second-order derivatives efficiently.

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Aquatic insects play a minor role in dispersing salmon-derived nutrients into riparian forests in southwestern Alaska

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Abstract: Recent research has highlighted the importance of nutrients derived from Pacific salmon (*Oncorhynchus* spp.) carcasses for coastal freshwater and riparian ecosystems. To investigate the role of emerging aquatic insects in dispersing salmon nutrients from spawning streams to riparian habitats, we quantified the emergence and return rates of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) on Pick Creek in southwestern Alaska and, using stable isotopes, estimated the associated flux of nutrients derived from sockeye salmon (*Oncorhynchus nerka*) to streamside forests. Between June and September of 2004, 7.6 $mg \cdot m^{-2}$ of salmon-derived nitrogen emerged from Pick Creek in the form of aquatic invertebrates, 6.7 $mg \cdot m^{-2}$ of which was transferred to the terrestrial ecosystem. Dispersal patterns on four area streams showed that the majority of stream-borne nutrients are deposited within 25 m of the stream. Aquatic insects represent a minor vector for salmon nutrients to terrestrial systems, dispersing less than 0.03% of total nitrogen imported to Pick Creek by spawning salmon. Nevertheless, emerging insects make available salmon-derived resources otherwise inaccessible to some terrestrial consumers.

Résumé : Des recherches récentes soulignent l'importance des nutriments dérivés des carcasses de saumons du Pacifique (*Oncorhynchus* spp.) pour les écosystèmes côtiers d'eau douce et les écosystèmes des rivages. Afin de déterminer le rôle de l'émergence des insectes aquatiques dans la dispersion des nutriments de saumons depuis les cours d'eau de fraye vers les habitats du rivage, nous avons mesuré les taux d'émergence et de retour des éphémères (Ephemeroptera), des perles (Plecoptera) et des phryganes (Trichoptera) à Pick Creek dans le sud-ouest de l'Alaska; nous avons ensuite estimé le flux correspondant de nutriments dérivés des saumons rouges (*Oncorhynchus nerka*) vers les forêts riveraines à l'aide d'isotopes stables. Entre juin et septembre 2004, 7,6 $mg \cdot m^{-2}$ de nutriments provenant des saumons ont émergé de Pick Creek sous forme d'invertébrés aquatiques, dont 6,7 $mg \cdot m^{-2}$ ont été transmis à l'écosystème terrestre. Les patrons de dispersion dans trois sections du cours d'eau montrent que la majorité des nutriments provenant du cours d'eau sont déposés à moins de 25 m de la rive. Les insectes aquatiques représentent un vecteur peu important pour le transfert des nutriments provenant des saumons vers les systèmes terrestres et sont responsables de la dispersion de moins de 0,03 % de l'azote total importé dans Pick Creek par les saumons en fraye. Néanmoins, les insectes en émergence rendent disponibles des nutriments dérivés des saumons qui autrement seraient inaccessibles à certains consommateurs terrestres.

[Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) represent an important link between marine and freshwater ecosystems because of their anadromous and semelparous life history. Pacific salmon accumulate over 95% of their body mass in the marine environment (Groot and Margolis 1991), and their nutrient-rich carcasses are deposited in freshwater ecosystems upon their return migration, spawning, and eventual death. Recent evidence indicates that this seasonal pulse of energy and nutrients is an important subsidy to freshwater systems. Much attention has been drawn to the contribution by spawning salmon of marine-derived nutrients (MDN), including nitrogen (N) and phosphorus, which are incorporated into aquatic biota (Naiman et al. 2002; Schindler et al. 2003). Indeed, lotic organisms across nearly all freshwater trophic levels accumulate MDN relative to biota from streams or reaches inaccessible to salmon, including periphyton (Kline et al. 1990), invertebrates (Kline et al. 1990; Bilby et al. 1996), resident fishes (Wipfli et al. 2003), and juvenile salmonids (Bilby et al. 1998). While there is debate over the impact of MDN on the productivity of aquatic ecosystems, there exists some evidence that salmon carcasses in streams can increase the density of juvenile salmonids (Bilby et al. 1998) and some aquatic invertebrates (Wipfli et al. 1998; Lessard and Merritt 2006) at local scales.

Salmon-derived nutrients deposited in freshwater systems are also incorporated into terrestrial food webs and riparian

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forests (Ben-David et al. 1998; Willson et al. 1998; Helfield and Naiman 2001). Numerous terrestrial consumers feed directly on live and dead salmon (Cederholm et al. 1989; Ben-David et al. 1998; Willson et al. 1998). Terrestrial insects along stream reaches accessible to salmon are enriched in MDN relative to their counterparts collected from reaches blocked to salmon (Hocking and Reimchen 2002). Riparian vegetation along salmon-bearing streams or reaches is relatively enriched in ^{15}N compared with upland vegetation and vegetation adjoining reaches inaccessible to salmon (Reimchen et al. 2003; Bartz and Naiman 2005; Koyama et al. 2005), a contrast that suggests an association between spawning salmon and nutrient fluxes to terrestrial ecosystems.

Salmon nutrients are transported to riparian ecosystems via a suite of biotic and abiotic processes (Schindler et al. 2003; Helfield and Naiman 2006). Piscivorous predators carry salmon carcasses into riparian zones for consumption (Ben-David et al. 1998; Hilderbrand et al. 1999). Bears are perhaps the most conspicuous salmon predators and are responsible for the deaths of 5%–95% of salmon in streams (Reimchen 2000; Quinn et al. 2003; Gende et al. 2004). Consumers such as bears deposit salmon nutrients in riparian ecosystems through excretion (Hilderbrand et al. 1999) and often leave behind a substantial amount of unconsumed salmon tissue to decompose and enter riparian nutrient cycles (Reimchen 2000; Gende et al. 2004). Flooding also transports substantial numbers of salmon carcasses out of rivers and streams into adjacent riparian ecosystems (Cederholm et al. 1989). Salmon carcasses in some systems remain in aquatic habitats where they decompose, and riparian vegetation can take up dissolved MDN from both surface and subsurface (hyporheic) flow (Naiman et al. 2000; O'Keefe and Edwards 2003).

Emerging aquatic invertebrates may also be important vectors of MDN to riparian ecosystems. In mesocosms and natural experiments, larval forms of aquatic insects become enriched with salmon nutrients in the presence of salmon carcasses (Johnston et al. 1997; Chaloner and Wipfli 2002; Chaloner et al. 2002). Predatory and omnivorous insects, such as some caddisflies (Trichoptera) and stoneflies (Plecoptera), ingest salmon nutrients through direct consumption of salmon eggs and carcasses (Kline et al. 1993; Minakawa et al. 2002; Winder et al. 2005). Other invertebrates such as mayflies (Ephemeroptera) assimilate salmon nutrients indirectly by grazing on biofilms (Schuldt and Hershey 1995; Bilby et al. 1996). After emerging from streams, some aquatic insects disperse laterally into riparian habitats where they can potentially enter terrestrial food webs. Abundance of aquatic invertebrates generally declines with distance from streams (Griffith et al. 1998; Briers et al. 2002; Petersen et al. 2004), and this lateral dispersal pattern will control the extent to which aquatic invertebrates disperse salmon nutrients into riparian forests.

While it is widely accepted that Pacific salmon can influence terrestrial and aquatic food webs, we do not yet fully understand the extent and mechanisms of MDN movement into riparian habitats. In ecosystems where Pacific salmon have declined, restoration efforts include salmon carcass addition, under the assumption that the salmon-derived nutrients will be taken up in aquatic ecosystems as well as transferred to riparian habitats. Some of the vectors for nutrient transfer to riparian habitats have been investigated, most notably via the movement of carcasses to streamside areas by bears (Ben-David et al. 1998; Hilderbrand et al. 1999; Helfield and Naiman 2002). Other studies have proposed that emerging aquatic insects may also serve as a vector for the transfer of salmon-derived nitrogen (SDN) to terrestrial habitats (Reimchen et al. 2003; Schindler et al. 2003; Helfield and Naiman 2006; Merz and Moyle 2006). The purpose of this study was to quantify the role of aquatic invertebrates as vectors of MDN to riparian forests. We used N-stable isotopes to estimate the contribution of MDN to the biomass of three benthic invertebrate taxa. To determine the magnitude of the flux of MDN into riparian forests, we quantified emergence and return rates of aquatic insects on one salmon-bearing stream in southeastern Alaska and place our values in a broader context through a comparison with other published emergence rates. Finally, we also measured the lateral dispersal of aquatic insects in four study streams and thereby estimate the extent of transfer of stream nutrients to riparian forests. Our results show that from the perspective of mass flux, emerging aquatic insects play a minor and localized role in dispersing salmon-derived nutrients into terrestrial habitats.

Materials and methods

Study site

We sampled aquatic invertebrates during 2001 and 2004 in the Wood River lake system in the Bristol Bay region of southwestern Alaska (59°20′N, 158°40′W), a system characterized by high densities of sockeye salmon (*Oncorhynchus nerka*) in lakes and streams used as spawning habitat (Hilborn et al. 2003). The 20-year mean sockeye escapement for the Nushagak fishing district, including the Wood River system, was over 2.1 million for 1993–2003, over 60% of which returned to Wood River streams and lakes (Westing et al. 2005).

We sampled invertebrates on Pick Creek, a tributary of Lake Nerka that contains spawning sockeye salmon. The 10-year (1995–2004) mean sockeye salmon escapement to Pick Creek was about 6000 (D. Schindler, University of Washington Alaska Salmon Program, Seattle, Washington, unpublished data). Three additional Lake Nerka tributaries were used to study the spatial extent of invertebrate dispersal or to estimate mean invertebrate N isotopic values: Lynx Creek, with a 10-year mean sockeye salmon escapement of about 3500, and two streams without salmon, Cottonwood and Rainbow creeks (Table 1). Riparian vegetation on Lake Nerka tributaries is dominated by ferns and willow (*Salix* spp.), cottonwood (*Populus* spp.) and alder (*Alnus* spp.) shrubs and trees. Upland forest community is dominated by white spruce (*Picea glauca*).

Invertebrate sampling

To quantify the enrichment in SDN of aquatic insects in salmon-bearing streams of the Wood River system, we collected adult invertebrates during 2004 from Pick Creek and two non-salmon streams, Cottonwood and Rainbow creeks, for reference. Invertebrates were sampled between June and September, before, during, and after salmon spawning, using

Table 1. Physicochemical characteristics of study streams in Bristol Bay, Alaska.

Stream	Total length (km)	Mean channel width (m)	Mean depth (m)	Flow ($m \cdot s^{-1}$)	Slope (%)^e	Mean temperature (°C)	Conductivity ($mS \cdot cm^{-1}$)^d
Pick Creek	4.0^a	11.2^a	0.7^a	0.5^b	0.60	7.5^b	55.1
Lynx Creek	2.3^a	14.2^a	0.9^a	0.7^b	0.82	11.2^c	37.5
Cottonwood Creek	2.3^e	5.5^b	0.24^b	0.4^b	NA	8.7^d	25.0
Rainbow Creek	7.9^e	15^d	0.23^d	1.7^d	NA	8.0^d	41.9

Note: Flow is calculated as mean flow for June–September 2004, except for Rainbow Creek, where flow was measured on one day in September 2005. Depth and width for Cottonwood and Rainbow creeks are point measurements. Conductivity is corrected to 25 °C. No slope calculations were available for Cottonwood or Rainbow creeks (i.e., NA).

[a] G. Pess, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA, unpublished data.

[b] J.W. Moore, unpublished data.

[c] R.A. Marriott 1964.

[d] G.W. Holtgrieve, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA, unpublished data.

[e] T.B. Francis, unpublished data.

emergence traps and settling nets. Specimens were dried at 50 °C and finely ground, and a subsample of between 0.8 and 1.2 mg was used for determination of stable isotope composition. A Europa C/N continuous flow isotope ratio mass spectrometer was used to determine stable N isotopic ratios and total N content at the University of California – Davis Stable Isotope Facility (Davis, California).

The ratio of $^{15}N:^{14}N$ is used to calculate $\delta^{15}N$ as

$$(1) \qquad \delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] \times 1000$$

where R_{sample} is $^{15}N:^{14}N$ in the sample, and $R_{standard}$ is $^{15}N:^{14}N$ in the atmosphere (Peterson and Fry 1987). Mean $\delta^{15}N$ and total N content were calculated for the three dominant aquatic invertebrate orders collected, Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), for Pick Creek and across the two non-salmon streams.

To estimate the proportion of SDN incorporated into individuals of each invertebrate order, we used a two-source mixing model to determine the relative importance of N derived from salmon versus N derived from freshwater sources in insect tissues:

$$(2) \qquad \delta^{15}N_{insect} = P_{salmon}(\delta^{15}N_{salmon} + \beta L) + (1 - P_{salmon})(\delta^{15}N_{insect\text{-}ns})$$

where $\delta^{15}N_{insect}$ is the mean $\delta^{15}N$ of the target insect order collected from salmon-bearing streams; P_{salmon} is the proportion of insect N derived from salmon; $\delta^{15}N_{salmon}$ is the $\delta^{15}N$ of sockeye salmon tissue, assumed to be 11.2 ‰ (standard deviation (SD) = 0.45; Schindler et al. 2005); $\delta^{15}N_{insect\text{-}ns}$ is the mean $\delta^{15}N$ of the same insect taxa collected from non-salmon streams, where none of the N is assumed to be derived from salmon; β is the average enrichment in $\delta^{15}N$ between trophic levels (assumed to be 3.4‰; Post 2002); and L is the number of trophic levels between the consumer and the prey source.

Because we did not know the detailed trophic structure of our study streams, we generated scenarios of taxa-specific trophic positions to estimate a range of invertebrate enrichment in salmon nutrients, using the observed mean isotopic values for each insect order and a range of values for L (eq. 2) from 1 to 3. For example, when estimating the enrichment in SDN of stoneflies, we allowed for the possibility that they accumulate SDN either directly from consumption of salmon carcasses ($L = 1$; Chaloner et al. 2002) or indirectly through consumption of prey that ingest SDN directly. For example, the scenario with $L = 3$ characterizes a system where the stonefly is a secondary carnivore in a system where algae assimilate SDN directly (i.e., algae – grazer – primary carnivore – stonefly). The assumption of direct salmon consumption ($L = 1$) provides the highest estimate of enrichment, whereas assuming several trophic steps between salmon and consumers in the mixing model (i.e., $L = 3$) provides the most conservative estimate of enrichment. In this way, we can account for potential variation in trophic structure between study streams and bound our estimates of SDN enrichment in aquatic insects. Both methods provided similar estimates of the percentage of invertebrate N that was derived from salmon (see Results). A list of the aquatic invertebrate taxa in the four study streams is presented in Table 2.

To quantify the flux of SDN by emerging aquatic insects, we intensively measured emergence and settling rates of adult mayflies, stoneflies, and caddisflies on Pick Creek from June through September 2004. Emergence was measured continuously from 24 June to 10 September using 15 emergence traps at five sites along a 1000 m stretch of the stream, within the area of the stream used by salmon for spawning. Emergence traps were 0.25 m^2 boxes made of hardware cloth, anchored to the stream beds with rebar, and covered with 1 mm mesh mosquito netting that allowed flow of air and water. At each sampling site, emergence traps were placed along the edge and in the middle of the stream to capture possible variability associated with habitat type. Emergence rates were calculated as the mean number of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera) emerging per square metre of Pick Creek per day, multiplied by the mean individual mass per taxa. Because of uneven distribution in emergence rates of mayflies (Ephemeroptera) between habitat type (analysis of variance (ANOVA): $p < 0.001$; SYSTAT 11.0, Systat Software Inc., Point Richmond, California), mayfly emergence rates were weighted by the proportion of the stream reach estimated to be composed of open channel (0.9) and edge (0.1).

We continuously measured insect return, or settling, on Pick Creek from 26 June to 24 July using 30 settling nets at the same five sites established for measuring emergence. Settling nets were adapted from the design of Jackson and Fisher (1986) and were 39.5 cm diameter conical nets at-

Table 2. Aquatic invertebrate taxa of Wood River system streams, Alaska.

Order	Family	Genus
Ephemeroptera	Baetidae	*Baetis*
	Ephemerellidae	*Drunella*
	Heptageniidae	*Cinygmula*
Plecoptera	Chloroperlidae	
	Nemouridae	
	Perlodidae	
Trichoptera	Limnephilidae	*Ecclisomyia*

tached to sturdy wire frames suspended 5–8 cm above and parallel to the water. The basket of each net drifted freely downstream, but was weighted down to keep it submerged. Settling nets were also placed in both edge and open channel habitats to capture potential variability in return rates by habitat type. Both emergence traps and settling nets were sampled on average every 48 h. Insects collected were either frozen or preserved in 95% ethanol. Insect return rates were calculated as the mean number of aquatic invertebrates settling per square metre of Pick Creek per day, multiplied by the mean individual weight per taxa. Because settling was measured only until 24 July, whereas emergence was measured until 10 September, to estimate seasonal flux of aquatic invertebrates we calculated a mean per-day settling rate as a percentage of emergence for the period 26 June – 24 July and applied that rate to the period from 24 July to 10 September to estimate total seasonal settling. The proportion of adult aquatic insects returning to the stream is relatively constant over the emergence season, with the exception of a brief period during peak emergence (Stagliano et al. 1998).

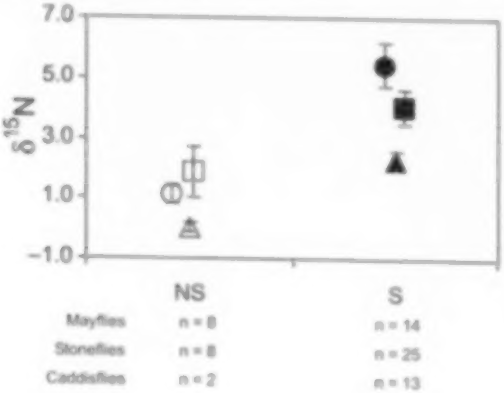
To establish a generalizable pattern of lateral aquatic insect dispersal following emergence, we sampled adult aquatic insects on four creeks during July and August of 2001, corresponding to time periods before and after salmon spawning. The majority of invertebrates on all streams emerged during the July sample period, and therefore those data were used to establish dispersal rates. We established sampling points along four transects on Pick, Lynx, Rainbow, and Cottonwood creeks at 0, 5, 10, 20, 50, and 100 m perpendicular to the stream edge. Adult insects were sampled at each sample point using a single sticky trap made of 345 cm^2 translucent plastic plates sprayed with Tangle-trap Insect Trap Coating (The Tanglefoot Company, Grand Rapids, Michigan) and suspended from vegetation ~1.5 m above ground. Traps were collected after 48 h, wrapped in plastic, and frozen. Insects were removed from sticky traps using Dumonde Tech Citrus Cleaner (Dumonde Design Group, Inc., Seattle, Washington) and rinsed twice in 95% ethanol before being preserved in 95% ethanol. Spatial distributions of aquatic invertebrates were calculated as the mean number of individuals collected per square metre of trap per 48 h period at each distance across all transects per stream. Dispersal results were separated by sample period (July and August) because of differences between sample times on each stream for at least one distance (ANOVA, $p <$ 0.001; SYSTAT 11.0). To estimate the lateral extent to which insects disperse nutrients away from each of the four study streams, we fit a logistic model to the number of insects found at increasing distance from the stream edge for each taxa, stream, and date. The proportion Y_X of insects found at distance X from the stream edge was characterized by the equation

$$(3) \qquad Y_X = 1 - \frac{1}{1 + \exp\left[-\ln(19)\left(\dfrac{X - p_{50}}{p_{95} - p_{50}}\right)\right]}$$

where p_{50} and p_{95} are fitted parameters that define the shape of the logistic model, and correspond to values of X that give 50% and 95% of the cumulative distribution, respectively. The models were fit by minimizing the sums of squares between the model and the observations taken on each of the study creeks. We used the resulting model fits for each insect order in each stream to quantify the distance at which 50% and 95% of insects were dispersed across all streams.

We used Helfield and Naiman's (2006) mass balance model for N flux in the Wood River system to compare emerging aquatic invertebrates against other vectors of SDN to riparian forests. We parameterized the model for Pick Creek stream area (2.4 ha) and salmon density (8200 in 2004). Parameters describing bear predation rate, hyporheic flow, precipitation, proportion of the riparian forest that is alder, and stream discharge were taken from Helfield and Naiman (2006).

Fig. 1. Nitrogen isotope signatures of stoneflies (circles), mayflies (triangles), and caddisflies (squares) on streams with no salmon (NS) and with salmon (S) in 2004. Symbols represent means of all individuals collected on each stream type. Error bars are ±1 standard error. Sample sizes for each taxa are listed below y-axis labels. All NS–S pairs are statistically different (Student's t test; $p < 0.05$).



Results

We compared enrichment in SDN of aquatic invertebrates collected from Pick Creek with those from two non-salmon streams. Caddisflies, stoneflies, and mayflies from Pick Creek were significantly ($p < 0.05$) enriched in ^{15}N relative to their counterpart taxa on non-salmon streams, as evidenced by their higher δ^{15}N values (Fig. 1). These mean δ^{15}N values were used in a two-source mixing model (eq. 2)

Table 3. Enrichment of aquatic invertebrates in salmon-derived nitrogen.

Taxa	Proportion salmon-derived N		*n*
	Direct consumption	Indirect consumption	
Stoneflies	0.32 (0.14)	0.21 (0.09)	25
Mayflies	0.16 (0.04)	0.11 (0.03)	14
Caddisflies	0.17 (0.09)	0.12 (0.06)	13

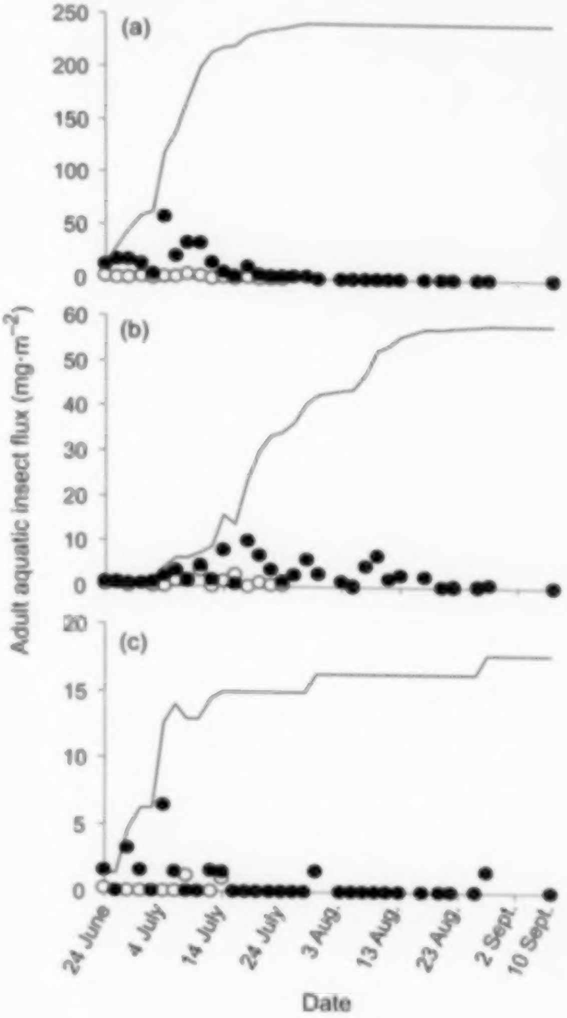
Note: Data shown are taxa-specific means (±1 standard deviation). Sample sizes (*n*) are the number of insects collected from salmon streams.

to calculate the proportion of N that is salmon-derived for the three insect orders (Table 3). We found that stoneflies on Pick Creek contained 21%–32% SDN, depending on which trophic structure scenario was imposed on the calculation. Enrichment in SDN was similar between mayflies (11%–16%) and caddisflies (12%–17%) on Pick Creek.

We intensively measured emergence and settling rates of three aquatic invertebrate taxa on Pick Creek in 2004. Emergence of mayflies and caddisflies peaked early in the season, on or about 4 July (Figs. 2*a*, 2*c*), whereas stonefly emergence peaked 2 weeks later, on or about 18 July (Fig. 2*b*). Emergence of these taxa from Pick Creek was 361.6 $mg{\cdot}m^{-2}$ over the entire season, or 4.8 $mg{\cdot}m^{-2}{\cdot}day^{-1}$ (Table 4). Mayflies represented the majority of the measured invertebrate biomass and nutrients emerging from Pick Creek, at over three times the emergence rate of the other two taxa (Table 4). Over the entire stream, 33.4 $mg{\cdot}m^{-2}{\cdot}season^{-1}$, or 9.2% of emerging aquatic insect biomass settled back into Pick Creek (Table 4), resulting in a net export of 328.2 $mg{\cdot}m^{-2}{\cdot}season^{-1}$ to riparian forests. Adult stoneflies had the highest rate of return to the stream (22.9%), as compared with caddisflies (10.9%) and mayflies (4.7%). Net seasonal flux to riparian forests over the entire season, calculated as the difference between seasonal emergence and seasonal settling, was highest in mayflies, followed by stoneflies and caddisflies (Fig. 2 cumulative line; Table 4). Mean (±1 standard error (SE)) individual dry mass per taxa was as follows: mayflies = 1.28 mg (0.1 mg); stoneflies = 1.06 mg (0.1 mg); caddisflies = 3.5 (0.9).

Using the stable isotope and mixing model results above, we calculated the flux of total N and SDN from Pick Creek by emerging aquatic insects. Of the 328 $mg{\cdot}m^{-2}$ total invertebrate biomass dispersed to riparian forests in 2004, 35.5 $mg{\cdot}m^{-2}$ of N was exported, of which 6.7 $mg{\cdot}m^{-2}$ was salmon-derived (Table 5). The SDN flux by emerging aquatic insects represented <0.01% of the 600–673 kg N imported by spawning sockeye salmon to Pick Creek in 2004, based on 8200 salmon returning (D. Schindler, unpublished data) and a conservative estimate of 73 g of N per salmon (Mathisen et al. 1988). Mean (±1 SD) proportion N by mass for each taxa were as follows: caddisflies = 0.11 (0.04); mayflies = 0.11 (0.04); stoneflies = 0.10 (0.03).

Fig. 2. Emergence (●) and settling (○) rates of adult mayflies (*a*), stoneflies (*b*), and caddisflies (*c*) on Pick Creek. Circles represent mean fluxes of dry mass per square metre of stream per day. Solid lines represent cumulative net flux of dry mass. Dips in cumulative net flux lines represent days with greater settling than emergence, resulting in a decline in total net flux to riparian forests.



We measured adult insect dispersal on four streams in 2001 to estimate the spatial extent of SDN exported by aquatic insects (Fig. 3). On Pick Creek, for example, dispersal of stoneflies, mayflies, and caddisflies declined exponentially with distance away from the stream edge (Fig. 3). Logistic model fits to cumulative dispersal patterns on all four study streams showed that adult aquatic invertebrate density was highest at the stream's edge, 50% of invertebrate biomass was dispersed to within 10 m of the stream, and 95% of invertebrate biomass was dispersed to within 25 m of the stream (Fig. 3). No aquatic invertebrates were collected 100 m away from the edge of any of the four study streams.

Discussion

Relative to estimates of other fluxes of N from salmon streams to riparian systems, we found that emerging aquatic invertebrates represent a minor vector. Many studies have demonstrated that larval aquatic invertebrates become enriched in ^{15}N in salmon-bearing streams (Kline et al. 1990,

Table 4. Emergence and settling rates of aquatic insects on Pick Creek, Alaska.

Taxa	Daily emergence ($mg \cdot m^{-2} \cdot day^{-1}$)	Seasonal emergence ($mg \cdot m^{-2} \cdot season^{-1}$)	Seasonal settling ($mg \cdot m^{-2} \cdot season^{-1}$)	Net seasonal flux ($mg \cdot m^{-2} \cdot season^{-1}$)
Mayflies	3.48 (0.8)	261.1 (62.0)	12.4 (5.9)	248.7 (57.4)
Stoneflies	1.12 (0.2)	84.0 (14.4)	19.2 (8.1)	64.8 (19.5)
Caddisflies	0.22 (0.1)	16.5 (7.8)	1.8 (1.8)	14.7 (8.5)
Total	4.8 (0.8)	361.6 (57.8)	33.4 (9.5)	328.2 (54.0)

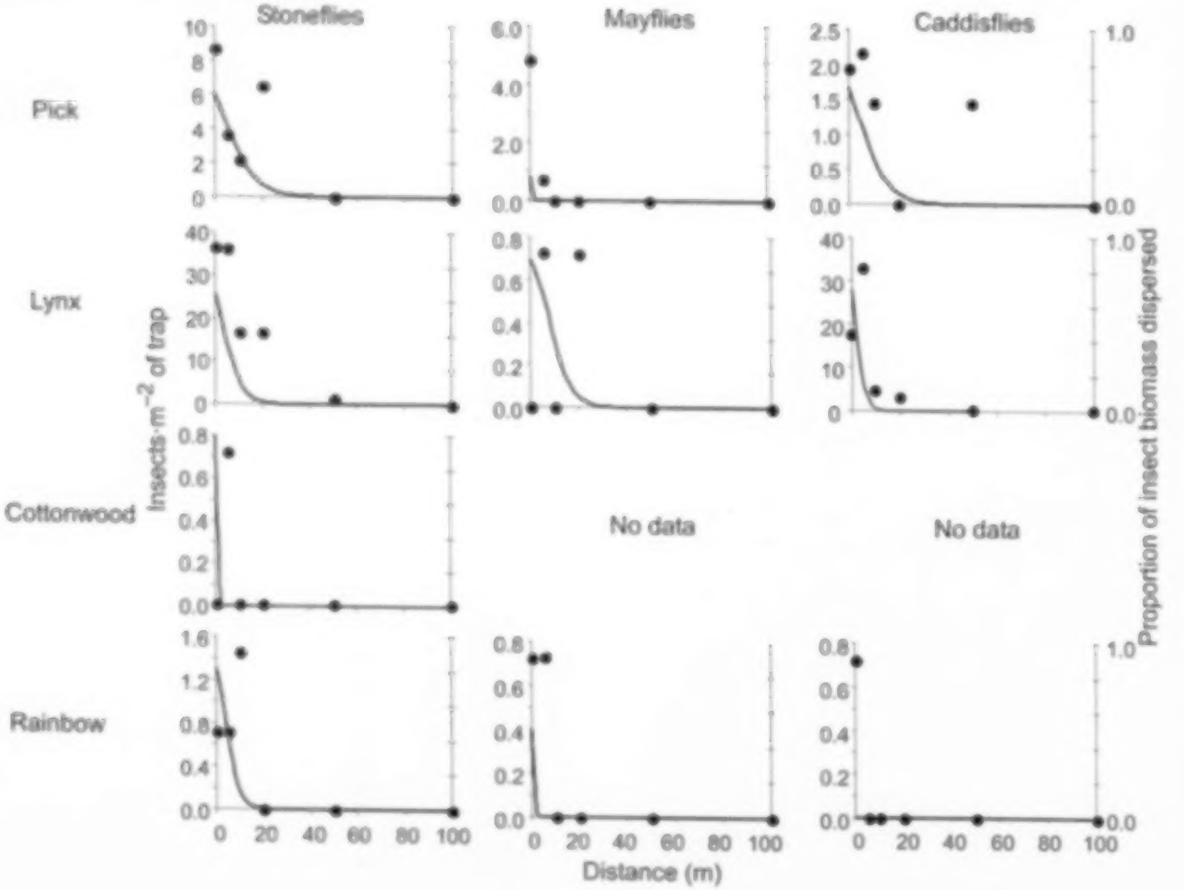
Note: Seasonal values are calculated from 24 June to 10 September. Shown are mean (±1 standard error).

Table 5. Seasonal fluxes of aquatic insect biomass and nutrients on Pick Creek, Alaska.

Taxa	Mass flux ($mg \cdot m^{-2} \cdot season^{-1}$)	N flux ($mg \cdot m^{-2} \cdot season^{-1}$)	SDN flux ($mg \cdot m^{-2} \cdot season^{-1}$)	N imported by salmon ($kg \cdot ha^{-1} \cdot year^{-1}$)
Mayflies	248.7 (57.4)	27.4 (6.3)	4.4 (1.0)	
Stoneflies	64.8 (19.5)	6.5 (2.0)	2.1 (0.6)	
Caddisflies	14.7 (8.5)	1.6 (0.9)	0.3 (0.2)	
Total	328.2 (54.0)	35.5 (6.0)	6.7 (0.9)	600–673

Note: Shown are means (±1 standard error). Proportions of N (nitrogen) are given in the text. Proportions of SDN (salmon-derived N) per taxa are as in Table 3.

Fig. 3. Dispersal patterns of emerging aquatic insects into riparian forests of four Wood River streams. Pick and Lynx creeks have salmon (*Oncorhynchus* spp.), Cottonwood and Rainbow creeks do not. Panels show decline in density on sticky traps with distance (●) and modeled (trend line) cumulative dispersal for emerging aquatic insects in July, prior to salmon spawning. No mayflies or caddisflies were caught in traps on Cottonwood Creek.



1993; Bilby et al. 1996), and it has been postulated that the emergence of these enriched invertebrates is a potentially important source of SDN for terrestrial ecosystems (Schindler et al. 2003; Helfield and Naiman 2006). The magnitudes of other biotic and abiotic N vectors to riparian forests, such as precipitation, watershed leaching, fixation by alder, hyporheic flow, and bear activity, have been estimated for Lynx Creek in the Wood River system (Helfield and Naiman 2006). Using the mass balance model of Helfield and Naiman (2006), we calculated that the N exported by emerging aquatic insects to riparian forests is <1% of the total estimated 532.3 kg of N input to the riparian habitats of Pick Creek in 1 year, based on escapement values from 2004 (Table 6). The magnitude of the emerging aquatic insect vector is over 100 times less than inputs from bear activity, 50 times less than the amount of N fixed by alder, and 10 times less than estimated N inputs from precipitation. Further, based on an estimated 600–673 kg SDN imported by salmon per hectare of Pick Creek in 2004, or 1400–1600 kg of SDN imported to the entire stream, we calculated that aquatic insects transfer to riparian systems ~0.16 kg, or 0.01% of the SDN imported to Pick Creek by spawning salmon.

We found that aquatic macroinvertebrates in salmon-bearing streams of the Wood River system had generally lower enrichment in ^{15}N than has been observed in other studies of Pacific salmon ecosystems. We observed a mean mayfly δ^{15}N of 2.3 versus a published range of 6.4–8.4 (Bilby et al. 1996); mean stonefly δ^{15}N of 5.5 versus a range of 4.8–9.2 (Bilby et al. 1996; Chaloner et al. 2002); and mean caddisfly δ^{15}N of 4.0 versus published values of 5.2 (Hicks et al. 2005) and 4–6 (Winder et al. 2005). That the invertebrates in our study have lower δ^{15}N signatures than their counterparts in other studies can be explained in part by the lower δ^{15}N of sockeye salmon tissue as compared with some other Pacific salmon species. The isotopic signature of sockeye salmon tissue in the Wood River system, which is representative of sockeye salmon generally (S. Johnson, School of Aquatic and Fishery Science, University of Washington, Seattle, WA 98195, USA, unpublished data) is lower than that observed for coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon (Satterfield and Finney 2002), the dominant species in the above-referenced studies (except Winder et al. 2005). Regardless of the pathway by which SDN are incorporated, higher δ^{15}N values in the source tissue (i.e., salmon) would be trophically transferred and result in higher δ^{15}N in organisms taking up those nutrients. Additionally, each of the above-referenced studies was conducted on nymphal stages of each invertebrate taxa, while we measured enrichment in adults. It is not known what fractionation, if any, occurs during metamorphosis, but any ontogenetic shifts in isotopic ratios may also contribute to variation in isotopic signature between our results and others.

Approximately 9.2% of emerging aquatic invertebrates returned to Pick Creek, a higher rate of return than has been observed in other systems (Jackson and Fisher 1986; Gray 1989). While we do not have reliable emergence rates from other streams within the Wood River lake system to use for comparison purposes, the emergence rates we measured on Pick Creek fall within expected values based on a literature review (Table 7). Jackson and Fisher (1986) calculated that 3% of all invertebrates emerging from a Sonoran desert stream returned, and Gray (1989) estimated 1% return rates for aquatic insects in a prairie stream. However, in heavily vegetated streams and wetlands, Stagliano et al. (1998) observed that return rates may be higher (~25%), perhaps as a function of vegetation structure that restricts dispersal away from streams (Jackson and Fisher 1986; Petersen et al. 1999). Some dispersing invertebrates prefer wooded to open sites (Petersen et al. 1999), and vegetation along Pick Creek may influence the rate of return we observed.

Table 6. Estimates of nitrogen (N) inputs to the watershed associated with Pick Creek, Alaska.

Vector	Minimum value (kg N·year^{-1}·watershed^{-1})
Precipitation	9.1
Leaching from upland soils	328
N inputs by alder	43
Hyporheic flow	46
Bear activity	106
Emerging insects	0.85 (0.14)
Total	532.9

Note: Based on mass balance model from Helfield and Naiman (2006) and adjusted for Pick Creek values.

Using the relationship of invertebrate density versus distance for the three aquatic invertebrate taxa on four streams in the Wood River system, it was possible to calculate the total potential biomass dispersed at distance into the riparian forest. Model fits to the data compiled across all four streams indicated that 95% of emergent insect biomass was dispersed to within 25 m of the stream (Fig. 4). This is consistent with other observed patterns of aquatic invertebrate dispersal, for example in the United Kingdom, where a model of exponential decline explained 67%–99% of the variation of stonefly abundance with distance, and many species of stoneflies and caddisflies dispersed no greater than 50 m from their natal stream (Petersen et al. 1999). We observed some variance around the dispersal model fits, and specifically we observed equally high densities of caddisflies at 20 and 50 m on Pick Creek. However, on Pick Creek we caught limited densities of caddisflies in sticky traps, and across all streams caddisflies represented <6% of total emerging biomass. The majority of emerging aquatic invertebrate biomass was represented by mayflies and stoneflies, and therefore the caddisfly dispersal on Pick Creek contributes little to the overall pattern by which stream-borne nutrients are dispersed to riparian forests. Our data show that the influence of stream-borne nutrients on riparian forests due to aquatic insect dispersal is localized to an area within 25 m from the stream edge.

We observed variable aquatic invertebrate emergence patterns that may be relevant for terrestrial consumers reliant on aquatic food resources. When aquatic invertebrates disperse into riparian forests, they can become a key component of terrestrial food webs as a prey source for consumers such as birds and spiders (Nakano and Murakami 2001; Sanzone et al. 2002). Emergence on streams is typically seasonal and spatially organized such that emerging insects are at higher densities near the stream edge (Jackson and Fisher 1986).

Table 7. Published emergence rates of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) for various sites worldwide.

Taxa	Site	Location	Stream temperature (°C)	Emergence ($mg \cdot m^{-2} \cdot day^{-1}$)	Reference
Ephemeroptera	Sycamore Creek	33°N, 111°W	15–25	27.3	Jackson and Fisher 1986
	Balsam Hollow Brook	46°N, 63°W	6–17	5.1	Dobrin and Giberson 2003
	Lake Belau	54°N, 10°E	5.5–16	0.21	Poepperl 2000
	Pick Creek	59°N, 158°W	5.5–16	3.41	This study
Plecoptera	Balsam Hollow Brook	46°N, 63°W	6–17	18.5	Dobrin and Giberson 2003
	Broadstone Stream	51°N, 0°E	5–17	3.99	Petersen et al. 1999
	Lake Belau	54°N, 10°E	6–17	0.005	Poepperl 2000
	Central Jutland	56°N, 9°E	5.7–6.4[a]	1.7–4.3	Thomsen and Friberg 2002
	Pick Creek	59°N, 158°W	5.5–16	1.07	This study
Trichoptera	Balsam Hollow Brook	46°N, 63°W	6–17	2.5	Dobrin and Giberson 2003
	Lake Belau	54°N, 10°E	6–17	2.42	Poepperl 2000
	Pick Creek	59°N, 158°W	5.5–16	0.27	This study

Note: Sites are organized by increasing latitude.

[a] Range of mean temperature values over several streams.

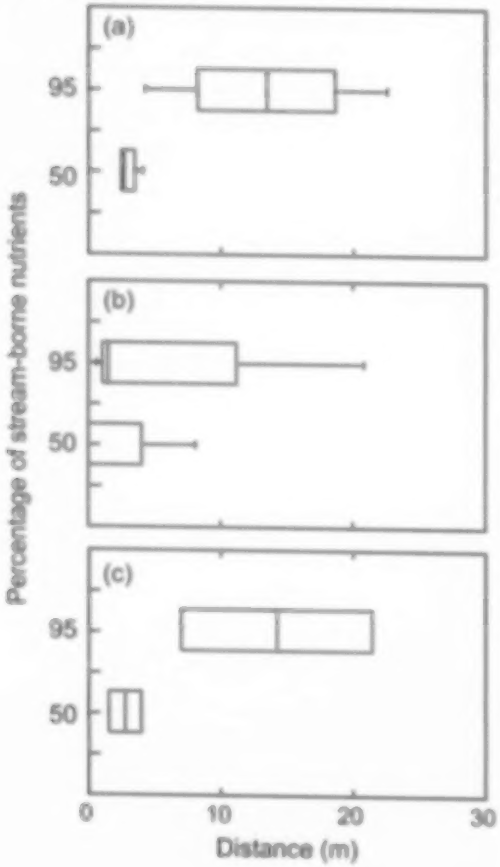


Fig. 4. Estimated mean distances to which 50% and 95% of stream-borne nutrients are exported by stoneflies (*a*), mayflies (*b*), and caddisflies (*c*) on Pick, Lynx, Cottonwood, and Rainbow creeks combined. Box plots are calculated from modeled dispersal patterns given in Fig. 3.

This aquatic subsidy can affect spatial aggregations of consumers, in some cases affecting their behavior or growth (Baxter et al. 2005). Insectivorous birds have been shown to be dependent on the subsidy provided by emerging aquatic insects (Gray 1993; Nakano and Murakami 2001), and the response of the insectivore community to this subsidy can be focused on streams that support spawning salmon (Gende and Willson 2001). A review of the phenology of several of the dominant passerine species found near Pick Creek showed that most have initiated fledging by 15 July in higher latitudes (Peck and James 1987; Petersen et al. 1991; Robertson et al. 1992). Emergence across all three insect taxa prior to 15 July equaled 78% of total seasonal emergence. This substantial and early pulse of emergence may result in a focused predatory response by insectivorous birds, whose nesting and rearing periods coincide with the peak emergence of insects, representing substantial quantities of salmon-derived nutrients and energy. More investigation into the taxonomic variability in phenology and emergence, which has been observed in other systems (Huryn and Wallace 2000; Dobrin and Giberson 2003), may demonstrate variable availability of SDN to terrestrial consumers in this system.

While our results suggest that aquatic invertebrates are not substantial vectors of salmon nutrient transfer from streams to riparian ecosystems on a watershed scale, their emergence may still be an important link between aquatic and terrestrial ecosystems in that they provide a prey subsidy for terrestrial insectivores. Emerging insects enriched in SDN make accessible marine nutrients that might otherwise be unavailable to consumers reliant on terrestrial insects. Furthermore, our study did not measure emergence rates or enrichment of aquatic Diptera, which may represent a substantial portion of total emergence from these streams and therefore a key prey item for terrestrial insectivores. Future research to investigate the marine–aquatic–terrestrial linkage in these systems should be conducted with active insectivore communities whose breeding seasons coincide with the presence of spawning salmon, for example passerine birds.

Currently, many runs of Pacific salmon and steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) are either threatened or endangered, and Pacific salmon stocks have disappeared from over 40% of their historical ranges (National Research Council 1996). The majority of research on Pacific salmon has focused on the salmon themselves. However, recently the ecosystem-level impacts of salmon have become more widely recognized, and research efforts are shifting to include salmon in an ecosystem context. The recent intense focus on salmon as deliverers of nutrients to aquatic ecosystems has identified several routes by which salmon nutrients are incorporated into aquatic biota. However, evidence that this flux of nutrients substantially affects aquatic ecosystem productivity is more equivocal, and in fact salmon may have equal or greater impacts on in-stream production in their role as ecosystem engineers (Moore 2006). As restoration and conservation plans for salmon are developed in areas where their populations have declined or where they have been eliminated, it is important that we clearly understand the linkages that exist between Pacific salmon and riparian and aquatic ecosystems.

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Tributary control of physical heterogeneity and biological diversity at river confluences

Stephen P. Rice, Robert I. Ferguson, and Trevor B. Hoey

Abstract: Investigations utilizing a one-dimensional sediment routing model demonstrate that moderate inputs of water and sediment at tributary junctions greatly increase physical heterogeneity in the recipient channel. Simulated physical heterogeneity is most sensitive to the ratios of tributary to mainstream bed load flux and bed load grain size and is less sensitive to relative discharge. Within the model, aggradation drives the processes that augment habitat variability, and in general, any aggradational confluence will be associated with elevated physical diversity. Model output reveals elevated physical diversity at two scales: between distinctive upstream and downstream zones separated by a confluence step and within each zone as a function of local environmental gradients. Total diversity increases as tributary sediment load and caliber increase relative to the mainstream. The ecological implications of the patterns and magnitude of tributary-induced physical heterogeneity are considered, and testable hypotheses are presented. Results highlight the need to accurately characterise patterns of sediment production, delivery, and routing in order to predict local tributary impacts and thereby understand patterns of habitat diversity and biodiversity at network scales.

Résumé : Des recherches utilisant un modèle unidimensionnel de transport des sédiments montrent que des apports modérés d'eau et de sédiments aux points de jonction des tributaires augmentent considérablement l'hétérogénéité du chenal récepteur. L'hétérogénéité physique simulée est très sensible au rapport des flux des charges de fond du tributaire sur ceux du cours principal ainsi qu'au rapport des tailles des particules; il est moins sensible aux débits relatifs. Dans le modèle, l'alluvionnement entraine les processus qui augmentent la variabilité de l'habitat et, en général, toute confluence d'alluvionnement est associée à une augmentation de la diversité physique. Les résultats du modèle montrent des augmentations de la diversité physique à deux échelles, soit entre des zones distinctes d'amont et d'aval séparées par un seuil de confluence, soit dans un même zone en fonction des gradients environnementaux locaux. La diversité totale augmente en fonction de l'accroissement de la charge et du calibre des sédiments du tributaire par rapport à ceux du cours principal. Nous examinons les conséquences écologiques des patterns et de l'amplitude de l'hétérogénéité physique générés par les tributaires et nous présentons des hypothèses testables. Nos résultats soulignent la nécessité de caractériser avec précision les patrons de production, de livraison et de cheminement des sédiments afin de pouvoir prédire les impacts locaux des tributaires et ainsi comprendre les patrons de diversité d'habitat et de biodiversité à l'échelle des réseaux.

[Traduit par la Rédaction]

Introduction

A growing body of evidence suggests that tributary confluences are significant biological locations within lotic ecosystems. Understanding how and why tributary confluences affect lotic ecology is vitally important for the development of local and basin-scale management strategies for these "hot spots" (cf. McClain et al. 2003). A significant issue is the extent to which different tributaries affect habitat heterogeneity in the recipient channel (Benda et al. 2004*b*). However, the controls of tributary-induced habitat diversity remain unclear. These controls are the general theme of this paper. We investigate tributary impacts on physical heterogeneity using a numerical model of the geomorphological processes that occur as water and sediment are added to a channel at a tributary junction.

The ecological importance of tributaries

The river continuum concept (Vannote et al. 1980) recognises tributary confluences as potential sites of perturbation along mainstream ecological gradients (Bruns et al. 1984; Minshall et al. 1985), and Perry and Schaeffer (1987) suggested that tributaries are sufficiently disruptive to define a river discontinuum. The link discontinuity concept developed this idea by proposing that patterns of water and sediment recruitment from tributaries configure an abiotic framework in which confluence nodes and the intervening channel links are basic spatial elements of biotic organiza-

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tion (Rice et al. 2001*a*). An important corollary is that ecosystem change along any drainage pathway is conditioned by the structure of the drainage network (Bravard and Gilvear 1996; Rice et al. 2001*a*). This is explicitly considered in the network dynamics hypothesis of Benda et al. (2004*b*) and the landscape-scale application by Poole (2002) of hierarchical patch dynamics (Townsend 1989; Wu and Loucks 1995). In both cases, it is argued that understanding confluence effects is an integral part of understanding aquatic ecology at landscape scales. It is in this context that tributary confluences have been explicitly identified as biodiversity hot spots (Benda et al. 2004*b*; Kiffney et al. 2006), which contribute disproportionately to overall aquatic biodiversity.

Spatially distributed ecological data to test these ideas are extremely rare (cf. Ganio et al. 2005), but there is field evidence to support the suggestion that confluence sites can be ecologically significant. For example, tributaries can reintroduce ecological complexity to otherwise impoverished environments downstream from river impoundments (Stevens et al. 1997; Greenwood et al. 1999; Vinson 2001) and on unregulated rivers may be associated with significant shifts in primary productivity, benthic community composition, and fish distributions (Knispel and Castella 2003; Kiffney et al. 2006). In addition, confluences can be sites of longitudinal community change (Fernandes et al. 2004) and may be favoured for particular ecological processes such as breeding (Kupferberg 1996).

There are a number of reasons that might contribute to the ecological importance of confluence zones, including (*i*) increased productivity due to tributary supply of supplemental nutrients, insect drift, and detritus (e.g., Wipfli and Gregovich 2002; Fernandes et al. 2004), (*ii*) tributary-induced changes in water quality characteristics (e.g., thermal regime, Milner and Petts 1994), and (*iii*) the juxtaposition of distinctive upstream, downstream, and tributary environments that enhance particular ecological processes such as spillover predation (Power and Dietrich 2002) and refugia use (Fraser et al. 1995). Here, we are primarily concerned with a fourth reason: that (*iv*) the recruitment of water and sediment from tributaries can produce geomorphological adjustments (Rhoads (1987) and many others) that increase physical heterogeneity in the recipient channel.

Physical heterogeneity is important for stream biota because of the well-established ecological principle that biological diversity tends to increase with environmental diversity. Indeed, a positive association between stream habitat complexity and species richness has been recorded in numerous studies (e.g., Downes et al. 1998). In turn, it is reasonable to suppose that confluences are, at least in part, ecologically important because of their role in promoting mainstream physical heterogeneity (Rice et al. 2001*a*; Benda et al. 2004*b*; Kiffney et al. 2006).

Not all tributaries produce mainstream adjustments, so a key question is, what controls tributary impact? That is, which tributaries are most likely to have an impact on the physical heterogeneity and thus ecology of the recipient streams? This is important for river management because it may help to target restoration and conservation strategies to particular parts of the channel network and to identify putative biological hot spots on the basis of geomorphological information (Benda et al. 2004*b*). However, our understanding of tributary-related geomorphological adjustments, and consequent changes in physical heterogeneity, remains extremely limited (Rhoads 1987).

What controls tributary impact?

Knighton (1980) argued that the receiving channel will be affected after a junction if a tributary supplies a substantial flux of relatively coarse bed load. Rice (1998) used grain size data from two Canadian rivers to confirm that tributary bed load caliber and flux are key controls and developed logistic regression models to predict the likelihood of tributary impact. Of 156 mainstream tributaries in the two river basins examined, 15% (23 tributaries) were associated with significant shifts in bed material texture. Useful independent variables were surrogates for water and sediment generation (relative basin area) and sediment delivery from the tributary (tributary stream power close to the confluence). Benda et al. (2004*a*) examined a larger database that included 167 sites and defined geomorphological significance more widely using morphological, as well as sedimentological, criteria. They also found that the frequency of significant impact increased with tributary size relative to the receiving channel and used logistic regression to model this effect. These models are useful but they only predict the likelihood of tributary impact, not the magnitude of the expected changes in particular physical characteristics. Moreover, they use gross surrogates (e.g., drainage basin area) for the factors that actually affect relevant geomorphological processes (bed load flux, sediment grain size distribution, water discharge) and therefore add relatively little to our fundamental understanding of the adjustment processes that are operating and the controls on the heterogeneity that these produce.

To develop understanding of tributary influence, we have created a sediment routing model, TRIB, which simulates the evolution over time of width-averaged bed elevation and bed material grain size distribution (GSD) for a channel that recruits water and (or) sediment from a tributary halfway along its length. The work described above, and other considerations, indicate that there are three key controls on tributary impact: the ratios of tributary discharge to mainstream discharge (QR), tributary bed load flux to mainstream flux (FR), and tributary bed load grain size to mainstream bed load grain size (DR). Elsewhere we report the results of work that used TRIB to assess the relative importance of these ratios for controlling mainstream geomorphology in the vicinity of confluences (Ferguson et al. 2006). We found that adjustments of bed elevation and grain size reflect the interplay between the additional bed load that is introduced and the ability of the recipient channel to transport it with the additional discharge.

Aims

In this paper, we use TRIB model simulations to examine how the three key controls QR, FR, and DR affect physical heterogeneity close to river confluences. Specifically, we ask how much physical heterogeneity is produced close to a confluence under different combinations of these factors and which factors are most important. We consider spatial variability throughout the confluence zone, as well as in the reaches immediately above and below the confluence. The model is run for generic scenarios that use sensible boundary conditions and we consider the sensitivity of our results to these boundary conditions and to parameters used in the model. Numerical predictions are specific to the experimental setup but the qualitative predictions are robust and consistent with field observations. They identify the relative importance of the key controls, the directions of their effects, and the ways in which they interact. Our approach is heuristic in that we aim to improve understanding of principles that are common to all river confluences, not to predict the characteristics of particular confluences. We therefore focus on the qualitative nature of the model predictions and use them to develop specific hypotheses concerning the implications for stream biota.

Materials and methods

Sediment routing model

TRIB is an iterative, process-form feedback model that is implemented in a spreadsheet package. The river channel is represented by bed elevation and GSD at 101 equally spaced nodes. At each time step, the model estimates local bed slope, flow depth, and bed load transport rate. If there is transport of sediment from one node to the next, bed elevations and bed material GSDs are updated accordingly at both nodes. Water and sediment are supplied in specified and steady amounts to the first node on the profile and at the 51st node (the tributary). Full details are given elsewhere (Ferguson et al. 2006).

In the following, subscripts "t", "u", and "d" refer to the tributary, upstream, and downstream reaches, respectively. Channel width (w) and discharge (Q) are constant along the upstream and downstream reaches, with a step change at the junction described by the standard regime relation $w_d = Q_d^b$, where $Q_d = Q_u + Q_t$. On the basis of extensive empirical evidence (e.g., Church 1992), the exponent b was set to 0.5. The bed GSD consists of five size fractions, set here as 0.25–1 mm ("sand"), 1–16 mm, 16–32 mm, 32–64 mm, and 64–128 mm. Bed aggradation or degradation is computed from the divergence in volumetric bed load flux using the overall Exner equation (Ferguson et al. 2006) solved using a simple finite-difference scheme with a time step small enough for numerical stability. Bed load transport rates are computed by the equations of Wilcock and Crowe (2003), although model trials with other transport laws gave the same qualitative results. The Wilcock and Crowe (2003) equations are especially appropriate here, being sensitive to the proportion of sand in the bed material, which is acknowledged as an important ecological parameter. Transport rates depend on the bed GSD and the shear stress (τ) exerted by the flow. TRIB calculates τ assuming quasi-uniform flow with Manning's resistance law and a constant value of bed roughness (n). This leads to the following equation for the shear stress exerted on the bed:

$$(1) \qquad \tau = \rho g (Qn/w)^{0.6} S^{0.7}$$

where ρ denotes water density, g is the acceleration due to gravity, and S is the channel slope. If the bed has a reverse slope, then a fixed and very small positive value is used for S in eq. 1; otherwise, no allowance is made for backwater effects. Other sediment routing models, for example, SEDROUT (Hoey and Ferguson 1994), solve the gradually varied flow equations that allow for backwater effects. Comparisons between SEDROUT and TRIB showed very little difference in results for typical idealised scenarios as reported here (Ferguson et al. 2006).

Model system and experiments

The main set of results was generated using boundary conditions and model parameters that are reasonable for gravel-bed rivers in temperate, piedmont settings: upstream width = 50 m, upstream discharge = 60 $m^3 \cdot s^{-1}$, n = 0.02, bed porosity = 0.3, and sediment density = 2650 $kg \cdot m^{-3}$. A 10 km long model domain, with the tributary entering at 5 km, was used throughout. We used additional sensitivity experiments to assess the generality of these results.

A spin-up procedure without any tributary inputs was used to develop a mutually adjusted longitudinal profile and bed sediment gradient, which then formed the starting point for our experimental runs. Spin-up began with a gently concave long profile that had a linear decrease in slope from 0.003 to 0.001 over the 10 km reach. Each node along this profile was characterised by the same typical symmetric gravel distribution with a fine tail added and a geometric mean diameter (D) = 32 mm. From this starting condition, the model was run with capacity bed load input to the first node and no tributary until monotonic downstream fining had developed along the profile and aggradation had declined to a very low rate everywhere (<0.01 $mm \cdot day^{-1}$). The resulting bed elevations and GSDs along the profile constitute a quasi-equilibrium state characterised everywhere by negligible rates of change in grain size and bed elevation — this is equivalent to the concept of a graded channel (Mackin 1948) wherein channel characteristics are adjusted to transport the water and sediment supplied without significant changes in morphology or texture. Immediately upstream of the confluence at node 50, the pattern of downstream fining that developed resulted in a geometric mean diameter of the bed material (D_u) = 26 mm. Hydraulic conditions here were typical of small gravel-bed rivers in flood: depth 0.69 m, velocity 1.75 $m \cdot s^{-1}$, shear stress 13.5 Pa (31% above the critical shear stress calculated using the equations of Wilcock and Crowe (2003)), and bed load flux 0.007 $kg \cdot m^{-1} \cdot s^{-1}$ (of which 58% was sand, giving a geometric mean diameter of the bed load (G_u) = 1.9 mm).

The experimental runs involved activating tributary inputs of water and sediment. Adding a tributary to a mainstream that is in quasi-equilibrium triggers morphological (aggradation or degradation) and textural (bed sediment coarsening or fining) adjustments that are initially rapid but slow down (see Ferguson et al. (2006) for an illustration). Perfect equilibrium is approached asymptotically over a very long period, so we used stopping rules similar to those described above for the spin-up procedure to define when simulations could be considered to be in quasi-equilibrium.

Ferguson et al. (2006) identified a primary distinction between conditions that led to channel aggradation or degradation at model confluences. Aggradation occurs where the downstream bed load transport rate is insufficient to remove all of the bed load supplied to the confluence because it is too coarse or too voluminous relative to the increase in hydraulic stress provided by increased discharge. Aggradation was the most common type of response for the wide-ranging permutations of QR, FR, and DR examined, and as a general rule, we found that aggradation occurred if a tributary supplied sediment appreciably coarser than the bed load being transported by the mainstream (DR > 2). The propensity for the simulated channels close to confluences to aggrade, rather than degrade, is consistent with field observations (Church and Kellerhals (1978), Rice and Church (2001), and others — see review in Benda et al. (2004*b*)). Strongly degrading confluences occur less frequently and require quite specific conditions that are relatively rare in nature: either a chronic supply of large volumes of very fine sediment (DR < 1), or a "clearwater" tributary that delivers large quantities of water but no sediment (FR → 0).

In the experiments herein, we focus on permutations of QR, FR, and DR that produce aggradation. We also simulated confluences with negligible changes in elevation, including very small amounts of degradation, because it is interesting to explore whether tributaries that appear not to have a significant geomorphological effect (which are common) nevertheless affect aspects of heterogeneity around a confluence. Negligible changes in elevation are associated with very small tributaries (QR ≤ 0.1 and FR ≤ 0.5) or with larger tributaries if the bed load caliber is similar to the mainstream load (DR = 1). We therefore examined ratios of QR = Q_t/Q_m from 0 to 1 (values 0, 0.2, 0.4, 0.6, 0.8, 1.0), the former representing a dry input, which could be a slug of sediment from a debris flow for example, and the latter representing a symmetric junction of two equal-sized streams. Tributary bed load flux is specified as a proportion FR of the mainstream flux 10 nodes above the junction, as linking it to mainstream flux closer to the junction can cause model instability. Simulations used FR in the range of 0.2 to 2.0 (values 0.2, 0.5, 1.0, 1.5, 2.0). Three alternative GSDs of the tributary bed load were used. The finest GSD with G_t = 1.9 mm is the same as the bed load GSD in the mainstream immediately upstream of the confluence. Two coarser bed load GSDs have G_t = 8 mm and 13 mm. DR = G_t/G_m and therefore ranges from 1 to ~7. The main set of experiments included 6 × 5 × 3 = 90 permutations of the controlling conditions.

Measuring spatial variability in habitat parameters

A variety of width-averaged physical habitat parameters can be calculated within the model, including depth, velocity, percentage sand, bed slope, and shear stress. For illustration, we examined the spatial variability of a substrate parameter and a hydraulic parameter: the geometric mean diameter of the bed material (*D*, mm) and the Froude number of the flow (Fd = $v/(g{\cdot}d)^{0.5}$, where *v* is mean velocity). Both of these parameters (or very closely related parameters such as the median bed grain size (D_{50})) have been shown to influence in-stream biotic processes and to affect, for example, the distribution of fishes at reach and river scales (Yu and Peters 1997; Lamouroux et al. 1999; Fleituch and Amirowicz 2005), the selection of spawning habitat by salmonids (Moir et al. 1998; Kondolf 2000; Milan et al. 2000), and egg-to-fry survival rates of salmonids (Rubin 1998; Bernier-Bourgault and Magnan 2002).

For each experimental run, the standard deviation of each of these variables (σ_{Fd}, σ_D) was calculated for the 10 nodes immediately above the confluence (km 4.0 to 4.9), the 10 nodes immediately below (km 5.0 to 5.9), and the 20 nodes in total (km 4.0 to 5.9). To quantify tributary impact on simulated heterogeneity, standard deviations were expressed as multiples of the equivalent standard deviations for the no-tributary situation (at the termination of the spin-up run). The ratios χ, α, and β quantify changes in spatial variability throughout the confluence zone (±1 km), above the confluence (–1 km), and below the confluence (+1 km), respectively. For example, for *D*

(2) $$\chi_D = \sigma_{D\ \mathrm{km\ 4\ to\ 5.9\ with\ tributary}} / \sigma_{D\ \mathrm{km\ 4\ to\ 5.9\ without\ tributary}}$$

(3) $$\alpha_D = \sigma_{D\ \mathrm{km\ 4\ to\ 4.9\ with\ tributary}} / \sigma_{D\ \mathrm{km\ 4\ to\ 4.9\ without\ tributary}}$$

(4) $$\beta_D = \sigma_{D\ \mathrm{km\ 5\ to\ 5.9\ with\ tributary}} / \sigma_{D\ \mathrm{km\ 5\ to\ 5.9\ without\ tributary}}$$

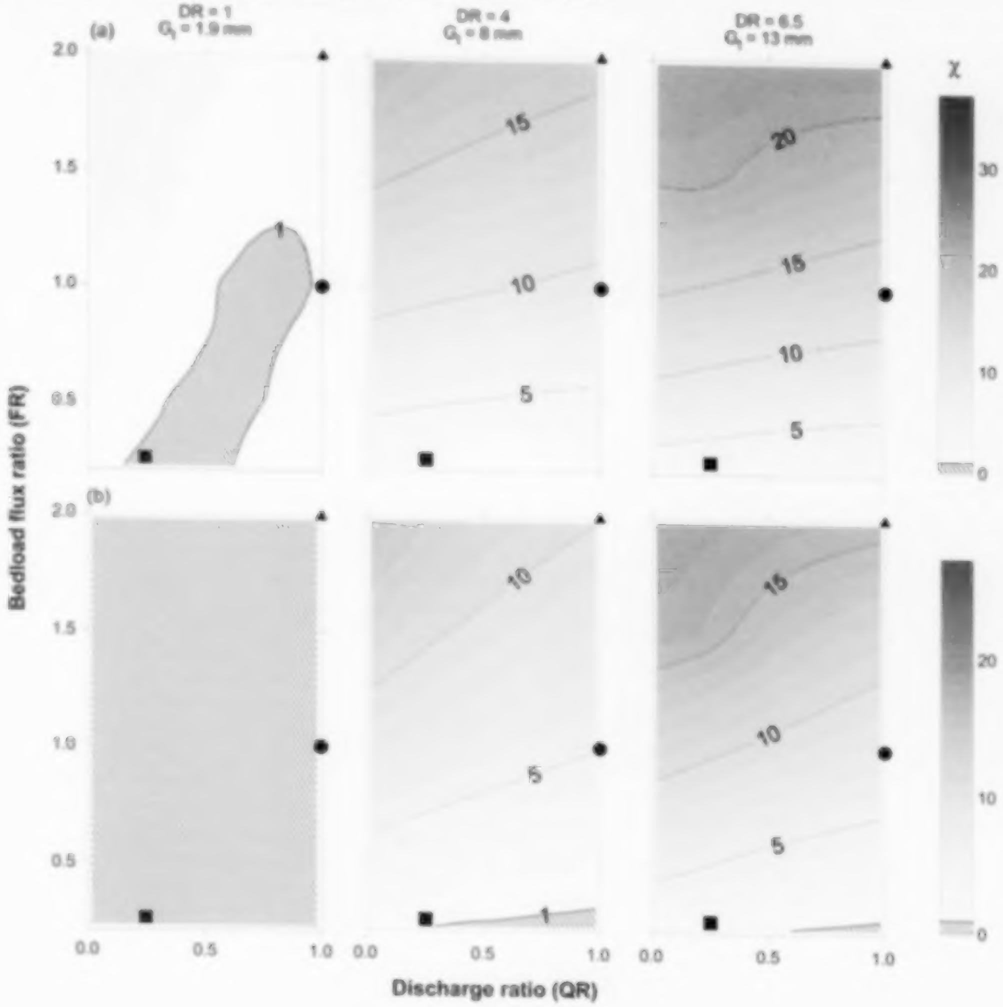
The ±1 km length corresponds to a scale larger than a channel width but substantially less than a channel link (a reach between successive tributaries), specifically 20 channel widths (or three to four riffle–pool cycles). This choice of scale is based on the following considerations: (*i*) a measurement scale greater than the width scale is sensible for a width-averaged model; (*ii*) although tributary-induced geomorphological adjustments ultimately occur at the scale of channel links, changes are most substantial in the vicinity of each confluence where responses to new water and sediment regimes are concentrated; (*iii*) characteristic scales of adjustment have not been determined empirically, although field experience is that adjustments occur over several pool–riffle cycles; and (*iv*) the chosen scale may be inappropriate for some biota, but it is not possible to specify a single scale that is relevant to all animals because different animals have widely differing spatial requirements.

Results

Heterogeneity throughout the confluence zone (±1 km)

Almost all of the experimental tributaries produced substantial increases in simulated physical heterogeneity throughout the confluence zone (Fig. 1). With the exception of some small tributaries that introduced fine bed load, variability of *D* increased relative to the no-tributary situation in all other model scenarios (Fig. 1*a*). Froude numbers became less variable (i.e., $\chi_{Fd} < 1$) for tributaries with the finest bed load input, but for almost all other simulations with coarser tributary bed load, variability substantially increased (Fig. 1*b*). In the model, increases in variability were not restricted to tributaries that introduced large amounts of water and sediment: modest tributaries also produce significant changes in heterogeneity. For example, with FR = QR = 0.25 (tributary bed load flux and water discharge 25% of the mainstream values), σ_D along the 2 km reach was twice as large as the no-tributary case for G_t = 8 mm and three times greater for G_t = 13 mm (Table 1, example 1). For a tributary carrying the same volume of water and sediment as the mainstream channel (FR = QR = 1.0), σ_D was nine times larger than the no-tributary value when G_t = 8 mm and 13 times larger for G_t = 13 mm (Table 1, example 2). For a tributary that carries the same volume of water but introduces twice as much sediment as the mainstream it joins (QR = 1.0, FR = 2.0), the respective increases in σ_D were 16 and 22 times (Table 1, example 3).

Fig. 1. Differences in χ as a function of QR, FR, and DR for (*a*) mean grain size (D) and (*b*) Froude number (Fd). χ (= with-tributary standard deviation (σ) / no-tributary σ) quantifies the change in spatial variability throughout the confluence zone (±1 km from the tributary) resulting from the tributary's presence. Isopleths are based on natural neighbour interpolation (an exact interpolator that also does not allow values outside the range of the data) applied to 30 pairs of FR and QR in each panel (see text for values). Darker shading indicates greater heterogeneity ($\chi > 1$), the contour representing no tributary impact ($\chi = 1$) is included, and a reduction in spatial variability ($\chi < 1$) is indicated by cross-hatching. Particular simulations used as examples in the text and tables are indicated by symbols: FR = QR = 0.25 (■); FR = QR = 1.0 (●); FR = 2.0, QR = 1.0 (▲).



Within the model, DR is an important control of tributary impact (Fig. 1; Table 2). When averaged across all permutations of FR and QR, σ_D was approximately 2, 10, and 13 times greater than without a tributary for G_t = 1.9, 8, and 13 mm, respectively. Simulated bed material heterogeneity is more sensitive to FR and less sensitive to QR as DR increases, and overall, FR is a more important control on χ_D than QR: contours in Fig. 1*a* lie almost parallel to the QR axis, especially for coarse tributary loads. It was only at G_t = 1.9 mm, when the sediment input was relatively fine, that discharge had a very strong influence and tributary bed load flux was relatively unimportant. These patterns are also evident for simulated Froude number variability. QR exerted somewhat more influence on χ_{Fd} than χ_D, but with the exception of the G_t = 1.9 mm case, gradients along the QR axis remain relatively modest, especially when the bed load input is coarse (Fig. 1*b*).

Thus, the variance of both bed material D and Froude number throughout the confluence zone is sensitive to the quantity and caliber of the tributary bed load but is less sensitive to tributary discharge, especially if the tributary supplies coarse sediment. Where a tributary supplied relatively fine sediment, close to the same caliber as the bed load in the mainstream, Fd was uniformly less variable than without the tributary and increases in the variability of D were small and restricted to a limited set of permutations of FR and QR.

Table 1. Values of χ for the entire confluence reach (= with-tributary standard deviation (σ) / no-tributary σ) for selected examples, standard runs (2 significant figures).

	G_t (mm)		
	1.9	8	13
Bed material, geometric mean, *D*			
(1) FR = QR = 0.25, χ_D	0.8	1.7	2.9
(2) FR = QR = 1.0, χ_D	1.1	9.1	13
(3) FR = 2.0, QR = 1.0, χ_D	1.3	16	22
Froude number, Fd			
(1) FR = QR = 0.25, χ_{Fd}	0.8	1.2	1.8
(2) FR = QR = 1.0, χ_{Fd}	0.6	5.0	7.7
(3) FR = 2.0, QR = 1.0, χ_{Fd}	0.8	10	18

Figure 1 also reveals that as FR increases, there is a tendency for the rate of increase of heterogeneity to slow down. For example, with G_t = 13 mm, as the flux ratio rises toward 100% of the mainstream flux (FR = 1), σ_D increases relatively rapidly to a value 15 times larger than the no-tributary case. However, it then stabilizes and increases only to approximately 21 times larger when the tributary flux is twice as large as the mainstream flux (FR = 2). It is possible that some limit is approached as FR increases, which, at high DR, can restrict heterogeneity across the zone.

Model runs used a simulated flood discharge that was necessary to build the geomorphology that defines bed material characteristics along the reach. However, most of the time, animals experience lower discharges and it is therefore relevant to ask what happens to the variance of Fd values along the reach if discharge is lowered once a quasi-equilibrium geomorphology has been achieved. We conducted additional experiments to explore this issue. We ran the model to quasi-equilibrium and then reduced the discharge to one-half and then one-quarter of the initial value used to grow the geomorphology. For these three hydraulic conditions, we compared the standard deviations of Fd values within 1 km of the confluence (σ_{Fd}). We repeated this experiment for the three permutations of QR and FR detailed in Table 1 (using G_t = 8 mm) in each of two model setups (the standard model and a setup using alternative hydraulic boundary conditions). In all six cases, σ_{Fd} values measured at the reduced discharges were almost identical to those measured at flood discharge, and increases in σ_{Fd} relative to the respective no-tributary situations were essentially unchanged. For example, using the standard model setup with QR = FR = 1 and G_t = 8 mm, there was a five times increase in σ_{Fd} at flood discharge (χ_{Fd} = 5.0) and an almost identical increase at the two reduced discharges (χ_{Fd} = 5.1 in both cases). Thus, at smaller, non-flood discharges the Fd heterogeneity remains elevated relative to the no-tributary case, and the degree of elevation is almost identical to that observed at the flood discharge used to generate the geomorphology. This illustrates that the impact of modeled tributaries on hydraulic heterogeneity is qualitatively independent of the discharge at which the hydraulics are reported.

Longitudinal patterns for QR = FR = 0.75

Spatially averaged measures of simulated heterogeneity are shown (Fig. 1). The spatial structure underlying this average behaviour can be assessed from changes in longitudinal mainstream variations. Downstream changes in bed elevation, *D*, and Fd are simple and monotonic in the absence of a tributary input. When a tributary is added and the model is run to a new quasi-equilibrium, new patterns emerge that reflect adjustment of the channel slope and bed texture to the imposed tributary inputs of water and sediment. Figure 2 illustrates how elevation, *D*, and Fd vary with distance downstream for the particular case FR = QR = 0.75, but for different values of G_t. The trends revealed in Fig. 2 are qualitatively similar to those for other scenarios.

Coarse sediment inputs (DR > 1)

For all G_t > 1.9 mm, the dominant feature of the modelled geomorphological adjustment is aggradation at the confluence because the mainstream can not transport away the coarser fractions of the tributary sediment load at rates that equal or exceed their rates of delivery. Progressive deposition at the confluence increases the slope immediately downstream, but reduces the slope immediately upstream, so the modelled long profile develops a discontinuity that resembles a knickpoint, but does not migrate (Fig. 2*a*). Aggradation occurs upstream of the confluence by deposition of sediment that can not be moved on the low gradient that develops there. In each model run, a unique quasi-equilibrium is attained when the slope below the confluence becomes sufficiently steep to move each sediment size at almost its rate of supply and aggradation becomes very slow. Higher gradients are required to generate shear stresses large enough to move the coarsest materials, so the total amount of aggradation increases with G_t (Fig. 2*a*).

For each new quasi-equilibrium, simulated sediment texture is finer than for the no-tributary case in the low-gradient channel upstream and coarser in the steeper channel downstream (Fig. 2*b*). Downstream, the coarsest sediment remains on the steepest slopes close to the confluence, and selective sorting (the propensity for finer sediments to outrun their larger counterparts) produces a downstream fining pattern and a concave longitudinal profile. Upstream, the reduction in slope is most acute close to the confluence so that the reduction in grain size is greatest here but lessens upstream. The confluence is then marked by a significant grain size step. These adjustments in slope and grain size are consistent with the patterns observed at sediment recruitment points on real rivers in a wide variety of environments (Rice and Church 1998, 2001; Benda et al. 2004*a*). The net effect of the grain size adjustments is a significant increase in the heterogeneity of the bed material within 1 km of the confluence.

The magnitude of the simulated grain size step and the length of the channel affected by the associated sediment sorting increase with the amount of aggradation and hence with G_t (Fig. 2*b*) and FR. In contrast, increasing QR while holding FR and DR constant increases sediment transport capacity, which reduces aggradation and leads to a reduction in χ_D. For example, if QR is increased by 50% to a value of 1.0 while FR is left at 0.75, χ_D declines slightly from 10.2 to 9.5 for the G_t = 13 mm case (Fig. 1*a*). In general, increases in the volume and size of supplied sediment promote aggradation, changes in slope, and sorting of sediment, whereas increases in discharge (water depth and shear stress) reduce aggradation by promoting sediment transport.

Table 2. Summary of average tributary-induced changes in the heterogeneity of the geometric mean grain size (D) and Froude number (Fd) along the entire confluence reach (±1 km) for standard runs (2 significant figures).

	G_t (mm)		
	1.9	8	13
(a) χ values			
Mean χ_D	1.7	9.6	13
Minimum–maximum χ_D	0.6–4.2	0.8–19	1.6–22
Mean χ_{Fd}	0.8	6.4	9.1
Minimum–maximum χ_{Fd}	0.6–1.0	0.5–15	0.5–18
(b) Ranges			
D, no-tributary range (mm)	2	2	2
D, mean with-tributary range (mm)	4	23	28
D, maximum with-tributary range (mm)	7	42	43
Fd, no-tributary range	0.1	0.1	0.1
Fd, mean with-tributary range	0.1	0.4	0.5
Fd, maximum with-tributary range	0.1	0.8	0.9

Note: Simulations for all permutations of FR and QR are lumped together and grouped by tributary bed load grain size, G_t ($n = 30$). χ = with-tributary standard deviation (σ) / no-tributary σ. Ranges are maximum to minimum values within the 2 km reach (±1 km from the tributary).

Within the model, patterns of change in Fd are similar to those for D, with an initial increase then decline downstream of the confluence and a reduction upstream of the confluence that lessens upstream (Fig. 2*c*). The downstream increase is in response to aggradation and steepening, which reduces water depth and increases velocity. Upstream, the reduction in slope leads to increased depth, reduced velocity, and lower Froude numbers (slower, deeper water). As with grain size, there is a step in Fd at the confluence and the net effect is a significant increase in the heterogeneity of flow characteristics within 1 km of the confluence. To our knowledge, detailed hydraulic data are not available to assess the realism of this pattern, though the experience of the authors is that slope reduction upstream of confluences is associated with extensive pool habitats, whereas steepening downstream is typically associated with extensive riffle and glides characterised by lower depths and higher velocities.

Because aggradation, via slope changes, causes greater differentiation of Fd, increases in G_t and FR are also associated with substantial increases in χ_{Fd} (Fig. 1*b*). The influence of QR on χ_{Fd} is less straightforward because modelled increases in discharge at a confluence act to increase depth and reduce aggradation, both of which reduce downstream Fd and its overall variability. Increasing QR in the absence of any other change therefore causes a reduction in χ_{Fd}. For example, increasing QR to 1.0 while holding FR at 0.75 leads to a reduction in χ_{Fd} from 6.2 to 5.4 for the G_t = 13 mm case. This influence is somewhat greater than the equivalent negative influence of QR on χ_D as indicated by the relatively greater influence of QR on patterns of χ_{Fd} in Fig. 1.

Fine sediment inputs (DR = 1.0)

In the model, mainstream response to the finest input, G_t = 1.9 mm (DR = 1.0; i.e., the same bed load grain size distribution in the tributary and mainstream), is in marked contrast to that of the coarser sediment inputs, because reductions in the variability of D and Fd are observed (Fig. 1). Without a tributary, Fd declines gradually downstream as velocity decreases and depth increases along the concave, equilibrium long profile (Fig. 2*c*). With the tributary, flow depth and velocity increase below the confluence to produce a slight increase in Fd relative to the no-tributary simulation (Fig. 2*c*). There are no significant changes upstream, so that over the entire confluence zone, Fd becomes more similar. The same response occurs for all QR and FR when G_t = 1.9 mm. Without a tributary, D becomes systematically finer downstream (albeit very slightly) in association with the concave equilibrium long profile. With the tributary, increased sediment transport capacity is sufficient to both remove the fine load introduced by the tributary and to accomplish slight erosion of the local bed (too small to discern in Fig. 2*a* but up to 0.02 m). Erosion involves preferential removal of fine material so that the simulated bed coarsens slightly downstream from the confluence (Fig. 2*b*). This coarsening, in the absence of any significant change upstream, reduces the overall range of D within 1 km of the confluence, hence the reduction in grain size variability ($\chi_D < 1$) for this combination of FR, QR, and DR. This response is common within a small subset of permutations (the zone of $\chi_D < 1.0$ in Fig. 1*a*) with DR close to 1.0 and FR = QR. Where QR exceeds FR by a factor of approximately 1.5, the relatively large water input generates greater excess transport capacity and sufficient bed coarsening to increase the range of D. In contrast, where FR exceeds QR by a factor of approximately 1.5, the load is too great to be removed by the modest increase in shear stress, leading to aggradation and fining of the bed downstream that is sufficient to ensure greater simulated variability than without the tributary.

Heterogeneity above the confluence and below the confluence

Within the model, tributary-induced increases in variability throughout the confluence zone result from changes that take place in the upstream and downstream reaches, as well

Fig. 2. Longitudinal patterns of (*a*) bed elevation, (*b*) mean grain size (*D*), and (*c*) Froude number (Fd) within 1 km of the confluence when QR = FR = 0.75 and for various G_t: 1.9 mm (short dash), 8 mm (long dash), and 13 mm (thick, solid line). The no-tributary cases (no trib.; fine solid lines) are shown for comparison. In (*a*), the 2 mm and no-tributary cases are almost indistinguishable.

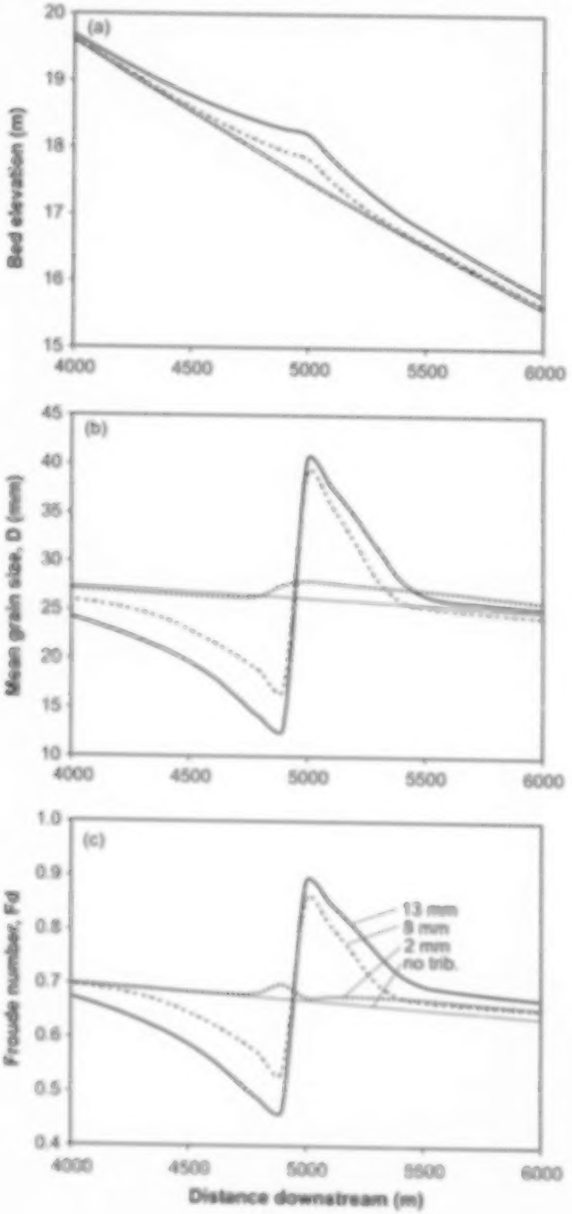


Table 3. Summary of average tributary-induced changes in the heterogeneity of the geometric mean grain size (*D*) and Froude number (Fd) in the kilometre upstream and downstream of the confluence for standard runs (2 significant figures).

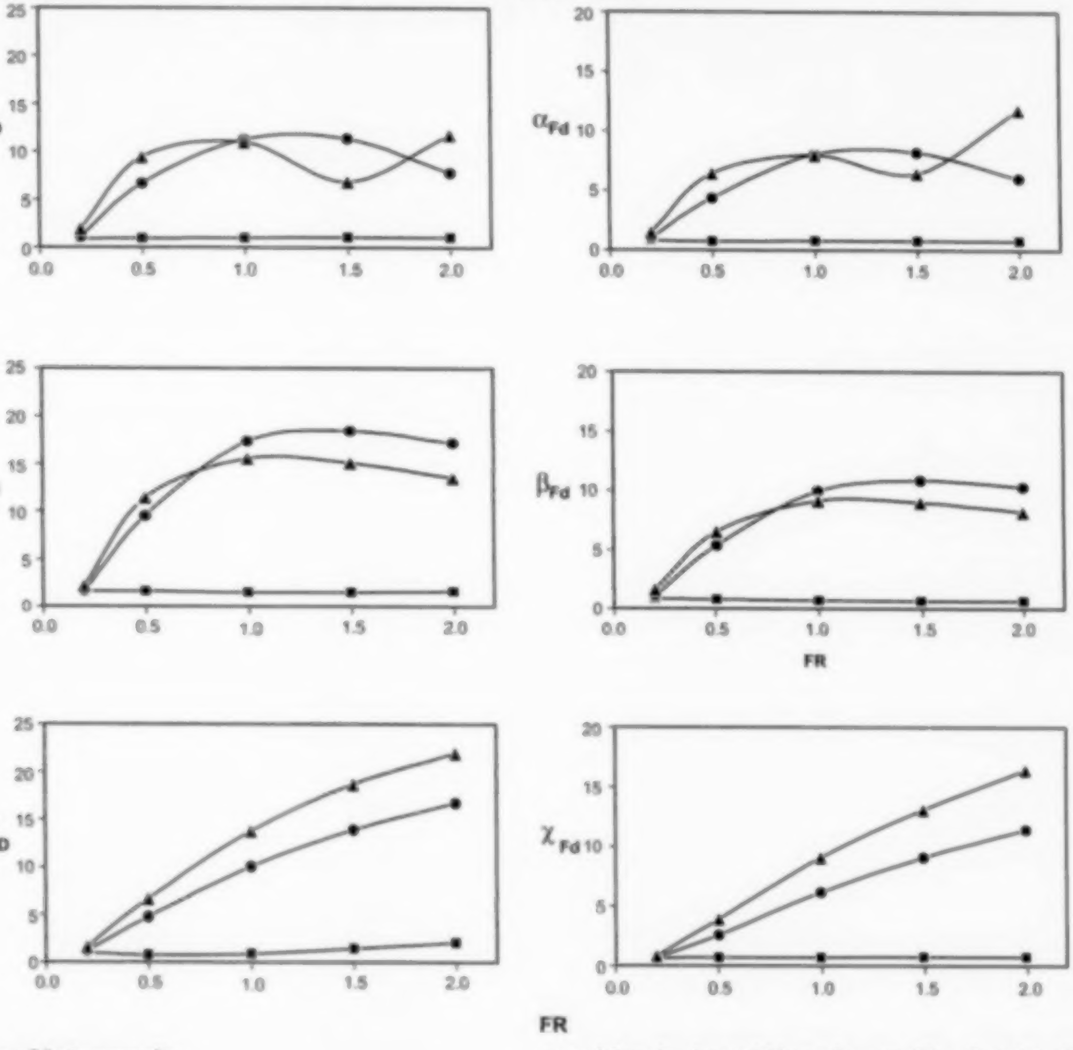
	G_t (mm)		
	1.9	8	13
Bed material, geometric mean *D*			
Upstream			
Mean α_D	1.1	7.8	8.7
Minimum–maximum α_D	0.9–1.9	0.9–12	1.0–12
Downstream			
Mean β_D	1.7	13	12
Minimum–maximum β_D	1.1–2.9	1.5–19	1.7–16
Froude number, Fd			
Upstream			
Mean α_{Fd}	0.9	5.8	7.3
Minimum–maximum α_{Fd}	0.8–1.1	0.8–11	0.9–12
Downstream			
Mean β_{Fd}	0.8	7.7	7.1
Minimum–maximum β_{Fd}	0.5–1.0	0.9–12	1.1–10

Note: Simulations for all permutations of FR and QR are lumped together and grouped by tributary bed load grain size, G_t (n = 30). α = with-tributary upstream standard deviation (σ) / no-tributary upstream σ; β = with-tributary downstream σ / no-tributary downstream σ.

as at the confluence. For all tributary simulations with DR > 1, variability increases in each reach (+1 km, –1 km) but these increases are less than for the entire confluence zone (±1 km), which also includes the influence of a grain size or Fd step at the confluence. Average α and β values are therefore smaller than the equivalent χ values for all simulations (Table 3; Fig. 3). For example, for G_t = 13 mm, average α_D and β_D are 8.7 and 11.7, respectively, whereas average χ_D is 12.9. It is instructive that values of α generally exceed 1.0 because it highlights the important influence of tributaries on the upstream, as well as the downstream, channel.

Figure 3 illustrates how α, β, and χ vary as FR and G_t change for simulations exemplified using QR = 0.6. Tributary-induced increases in overall variability χ become larger with FR throughout the range investigated, but increases in the upstream (α) and downstream (β) variability become larger only to FR = 1 and then oscillate or decline. Responses are broadly similar for other values of QR, and in general, as tributary sediment loads and the grain size of introduced sediment become larger, simulated variability in the upstream and downstream reaches tends to become more consistent and then decline. This happens for slightly different reasons in the two reaches. Upstream, there is a tendency for convergence in the quasi-equilibrium end points that the model channels reach. For example, with G_t = 8 mm, grain size patterns upstream of the confluence are very similar for FR = 1.5 and 2.0 (Fig. 4). Downstream, end-point profiles are slightly less consistent because larger volumes of coarse tributary sediment inevitably produce greater amounts of downstream aggradation. Here, the downstream variability of *D* and Fd declines as FR and G_t increase because the degree of local grain size coarsening on the steep slopes below the confluence is limited by the available sediment mixture and therefore approaches an upper ceiling. This first happens close to the confluence so that the locus of strong fining migrates downstream, eventually beyond the reach over which β is determined, and β values then decline.

Fig. 3. The response of tributary-induced changes in the heterogeneity of mean grain size (D), and Froude number (Fd) to changes in G_t and FR for cases with QR = 0.6. For each habitat variable, three plots show the change in standard deviation, as specified in eqs. 2–4, for the upstream reach (α), downstream reach (β), and entire confluence zone (χ). In each plot, FR varies on the abscissa and three lines represent different values of G_t: 1.9 mm (■); 8 mm (●); 13 mm (▲).



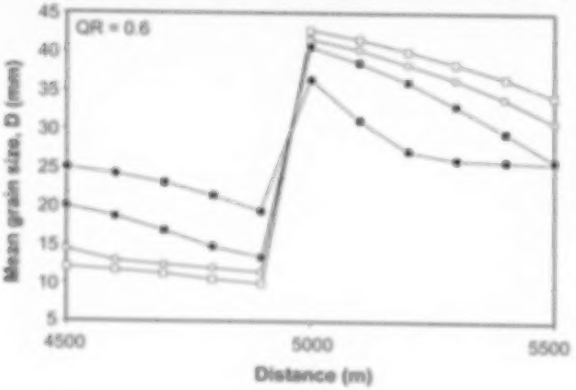
Patterns of heterogeneity

We suggest that heterogeneity is enhanced by tributaries at two scales (Figs. 2 and 4). First, abrupt discontinuities in channel gradient, bed sediment size, and flow properties occur at modeled confluences and produce two distinct habitat zones (upstream and downstream) where otherwise there would not be any zonation. The magnitude of this zonal differentiation is dependent on FR × DR, which quantifies the combined positive effects of increasing bed load grain size and bed load yield on aggradation (Fig. 5). As aggradation and therefore differentiation increase, the channel upstream develops a finer bed with higher sand content and deeper, slower flows (lower Fd), whereas downstream the simulated bed becomes increasingly coarse and clean with faster and shallower flows (higher Fd). A second scale of heterogeneity is evident in strong environmental gradients (e.g., in bed-material grain size) within each zone (Figs. 2 and 4). These are caused by adjustment processes such as downstream fining (Rice and Church (1998) and many others), which, again, are driven by aggradation.

Summary description of tributary-induced heterogeneity

To summarise the results of the large number of experimental runs, regression models were developed for χ_D and χ_{Fd} using QR, FR, and DR as independent variables. The values of the regression model coefficients are unique to the boundary conditions and parameter values used in the modeling scenarios and are not therefore reported here. However, the general form of the models and the relative explanatory power of the independent variables are of interest because these summarise the nature of the relations between tributary

Fig. 4. Longitudinal variations in grain size (D; mm) with QR = 0.6, G_t = 8 mm, and FR = 0.5 (●), 1.0 (■), 1.5 (○), and 2.0 (□).



characteristics and simulated mainstream heterogeneity. Models were developed only for DR > 1.0 because impacts on heterogeneity are trivial for DR < 1.0. FR and DR both have a positive influence on heterogeneity that can be adequately explained, so it is sensible to combine their effects into a single variable FR×DR. The ratio χ must be 1 when there is no tributary (FR×DR = QR = 0), so model intercepts were constrained to be 1.

Linear models including both FR×DR and QR provide the best fits and are significant ($p < 5 \times 10^{-6}$), with R^2 values of 0.94 and 0.97 (n = 60) for the χ_D and χ_{Fd} relations, respectively. The non-linear influence of FR×DR on channel heterogeneity (described above in relation to Fig. 3) is relatively weak for the data set as a whole. As expected, the influence of FR×DR on χ values is positive and the influence of QR is negative. FR×DR is the dominant independent variable, with standardized beta coefficients of 0.97 and 0.96 for χ_D and χ_{Fd}, respectively. QR coefficients nevertheless provide some additional explanatory power, especially in the χ_{Fd} relation where the standardised beta coefficient is –0.20 and inclusion of the QR term improves R^2 from 0.92 to 0.97.

Generality of results

The results described above are based on a large number of permutations of QR, FR, and DR spanning a wide range of tributary conditions, but using a standard set of boundary conditions (e.g., Q_u, w_u, the initial long profile, and bed GSD) and model parameters (e.g., Manning's n, width exponent b). Here we provide a single example of a sensitivity analysis that illustrates the impact of alternative boundary conditions and model parameters on modelling results. Additional sensitivity analyses, albeit focused on the general geomorphological response rather than physical heterogeneity, are reported in Ferguson et al. (2006).

In the standard experiments, initial mainstream conditions produce a shear stress of $\tau = 13.6\ N{\cdot}m^{-2}$ just upstream of the confluence, where the shear stress required to entrain the median grain size is $\tau_c = 10.4\ N{\cdot}m^{-2}$. We assessed the affect of changing the ratio τ/τ_c (= 1.31 for the standard case), which represents the initial competence of the mainstream channel close to the confluence. A selection of the standard permutations were repeated using the same channel width (w_u = 50 m) but mainstream discharges above the confluence of Q_u = 50 and 80 $m^3{\cdot}s^{-1}$ (instead of 60 $m^3{\cdot}s^{-1}$), so that shear stresses were lower and higher, respectively. Equation 1 shows that appropriate changes in slope, roughness, or channel width would have the same effect on τ. Results are qualitatively the same as in the standard runs: for fine G_t, negligible impacts, and for coarser sediment inputs, mildly non-linear increases in χ_D and χ_{Fd} as FR×DR increases and a relatively minor inverse effect due to changes in QR. The slopes of relations between χ values and FR×DR increase with Q_u (Fig. 6a), so that for a given combination of FR, DR, and QR, tributary-induced increases in heterogeneity are larger where mainstream competence is higher. These increases in heterogeneity are accompanied by, and explained by, increased aggradation at the confluence (Fig. 6b). Where mainstream conditions have higher values of τ/τ_c, confluence aggradation will be greater because the mainstream is competent to move coarser bed materials. Only the relatively coarse fractions of the introduced tributary load are retained at the confluence, and these require steep slopes (and therefore greater aggradation) to generate sufficient shear stress to move them on at their rate of supply. Thus, absolute mainstream hydraulic conditions (expressed as τ/τ_c) do have an impact on the magnitude of tributary-induced mainstream heterogeneity, but the nature of the impact is qualitatively consistent across a wide range of hydraulic conditions.

Discussion

The results of our modeling experiments can be summarised as follows. Fine-grained inputs (DR < 1) can reduce rather than increase heterogeneity around confluences, but for both D and Fd, they have only very minor impacts. In contrast, coarse-grained tributaries (DR > 1) increase simulated heterogeneity around confluences and can do so substantially. The key process that drives channel adjustment in the model and leads to greater heterogeneity in grain size and Fd is aggradation at the confluence, which increases channel slope downstream and reduces channel slope upstream, leading to grain size and flow adjustments. Relative tributary grain size (DR) and relative tributary sediment flux (FR) are more important controls of induced heterogeneity than relative discharge (QR). Larger values of DR and FR act to increase simulated heterogeneity because coarser grains and more voluminous supplies of sediment produce greater aggradation. In contrast, QR acts to reduce heterogeneity because it is associated with greater post-confluence sediment transport and therefore less aggradation. The positive influence of FR and DR on confluence zone heterogeneity is not strictly linear so that increments in variance become smaller as FR and DR become large. This is because of a convergence of channel conditions toward similar quasi-equilibrium profiles that impose a ceiling on overall variance. Also, variability close to the confluence may decline as FR and DR increase if aggradation at the confluence is sufficiently high to push the main loci of bed adjustment downstream, beyond the confluence zone.

Sensitivity tests illustrate that the magnitude of the simulated geomorphological adjustments is specific to the model setup and that changes in model parameters and boundary

Fig. 5. An illustration of the zonal differentiation between upstream and downstream habitats. Final (quasi-equilibrium) values of (*a*) mean grain size (*D*; mm) and (*b*) Froude number (Fd) as a function of FR×DR for positions 200 m downstream (×) and upstream (○) of the confluence (standard model simulations only). Each value is an average of the six QR conditions for a given FR×DR ± 95% confidence limits. Confidence limits are not shown if they are smaller than the size of the symbol. The difference between the two positions (●) is also shown and calculated as the average downstream value for given FR×DR minus the corresponding upstream average. The horizontal lines show the no-tributary values (broken line for upstream and solid line for downstream).

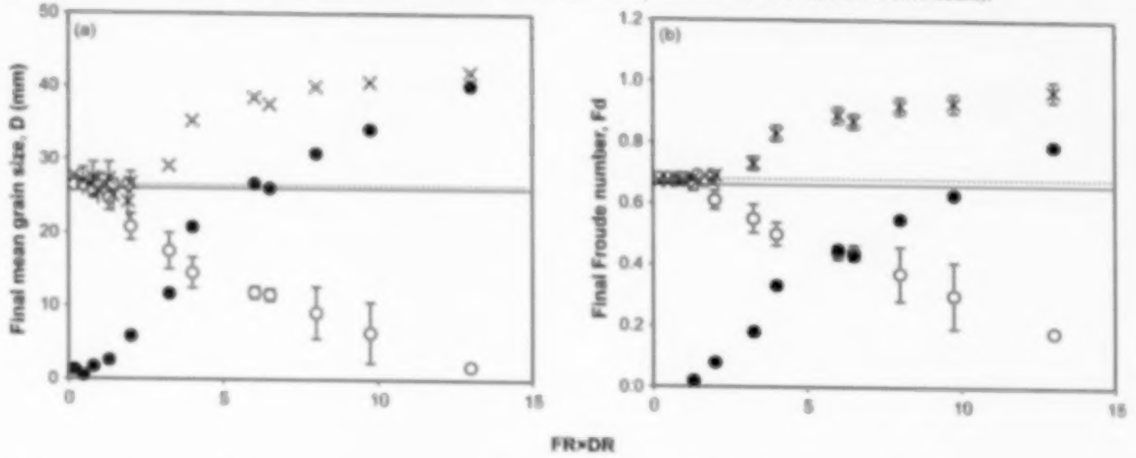
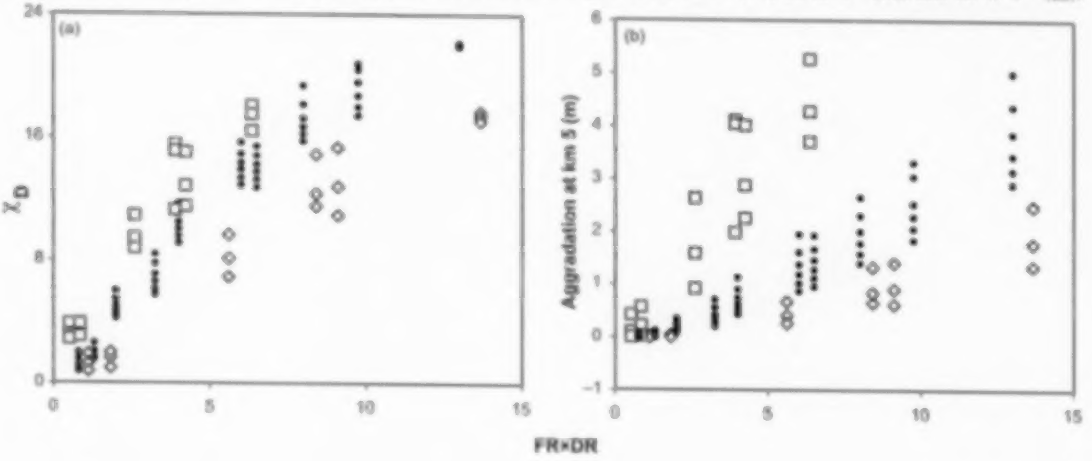


Fig. 6. Sensitivity to changes in mainstream discharge of (*a*) tributary-induced heterogeneity of mean grain size throughout the confluence zone (χ_D) and (*b*) tributary-induced aggradation at the confluence. Different discharge values reflect differences in mainstream competence (τ/τ_c). In each panel, data are plotted for mainstream discharges of 50 m^3·s^{-1} (◇), 60 m^3·s^{-1} (●), and 80 m^3·s^{-1} (□).



conditions affect the amount of simulated heterogeneity that is produced. The responses quantified in Figs. 1 to 6 and Tables 1 to 3 are therefore illustrative, rather than of predictive value. However, predicted impacts are qualitatively similar under different model setups, and for the large number of permutations that have been modeled, TRIB generates geomorphological adjustments that are qualitatively consistent with field observations (e.g., a grain size discontinuity followed by enhanced downstream fining). It follows that the modeling experiments are a useful heuristic tool for exploring the impact of tributaries on mainstream physical heterogeneity. The model results presented above provide rigorous information about the key controls on tributary-induced heterogeneity, the directions of their effects, the ways they interact, and their relative importance.

Making precise, quantitative predictions of absolute heterogeneity around real-world confluences is unlikely to be successful using a simple model like TRIB for at least two reasons. First, the model predicts channel conditions for a quasi-equilibrium condition, but in reality, sediment supply and, to a lesser extent, water supply are spatially discontinuous and temporally episodic. This introduces a degree of historical contingency and geographic complexity, which may mean that some confluences are not finely adjusted to local governing conditions (see Rice (1998) for examples). Second, the model uses a width-averaged one-dimensional representation of the channel, but in reality, lateral and vertical sorting processes augment heterogeneity by producing smaller-scale meso-habitat units that are not represented in the model. The interaction between the larger scale environmental controls and the smaller scale manifestation of important microhabitats is poorly understood and it is not possible to translate one-dimensional model output into quantitatively precise small-scale habitat metrics. Nevertheless, the qualitative results remain valid because small-scale units are nested within the larger-scale environmental patterns that the model captures and that define the available slopes, bed materials, and channel dimensions that two- and three-dimensional processes locally condition. That is, there is small-scale variability that the model does not capture, but this variance occurs about a mean local value that varies substantially along the reach and that the one-dimensional model predicts. In a field assessment, small-scale effects could be viewed as local phenomena and removed from assessments by using width-averaged field data.

These issues could be addressed by developing more complex models but these would inevitably incur greater information costs. More importantly, the benefits of doing so are not immediately apparent because the simple model used here provides useful, general insights into the controls of tributary-induced physical heterogeneity. In any case, currently there is no field data set that can provide an adequate quantitative test of modeling results, and any field test will be hindered by the difficulty of parameterising the key variables and determining their values for a large set of field confluences. In the absence of measurements of water flux, sediment flux, and bedload grain size (on time scales that would provide representative long-term values), it is inevitable that surrogates based on more easily measured parameters (e.g., basin area) would have to be used, introducing additional uncertainty to quantitative assessment of model performance.

Implications for in-stream biota

Many field and laboratory studies suggest that stream biota are sensitive to variations in the habitat parameters that we have examined (grain size and Froude number). For example, Yu and Peters (1997) found that fish in the Platte River, Nebraska, showed preferences for specific ranges of Fd, with some species found only at localities where $\mathrm{Fd} = 0$, $\mathrm{Fd} < 0.2$, or $\mathrm{Fd} < 0.3$. Lamouroux et al. (1999, 2002) and Lamouroux and Jowett (2005) have demonstrated a strong link between the trait composition of fish assemblages and reach-averaged Froude numbers. This link reflects the general association of low Fd (<0.2) with pool habitats and high Fd (>0.4) with riffle and glide habitats (Jowett 1993). Similarly, spawning salmonids are able to successfully utilize a wide variety of alluvial substrates (e.g., Kondolf and Wolman 1993; Milan et al. 2000), but high proportions of fine sediment impact egg incubation or fry emergence and overly coarse surface sediments preclude redd building, so substrate characteristics are a limiting factor. The median sizes of preferred gravels vary between species and with the size of individual animals, and the more diverse the array of available substrate mixtures, the more likely it is that salmon and trout of different species can find optimal sites for spawning success.

Our modeling predicts increases in the variability of these significant environmental characteristics due to confluences and we therefore anticipate a biological response, but it is difficult to quantify this response because (*i*) predictions about physical heterogeneity are qualitative, and (*ii*) quantitative relations between environmental characteristics and utilization by stream biota are not well defined, for example, by traditional reliance on central response modeling (Lancaster and Belyea 2006). Nevertheless, we are able to consider the likely implications of changes in physical heterogeneity and outline some testable hypotheses to guide future work in this area.

Our results suggest that tributaries enhance physical heterogeneity by creating distinctive upstream and downstream zones and by promoting the development of strong within-zone environmental gradients. Benda et al. (2004*b*) suggested that upstream "interference" and downstream "mixing" zones are likely to attract and support contrasting species and communities, thereby enhancing local biodiversity. There is some field evidence to support this. For example, along Pine and Sukunka rivers, Canada, significant changes in channel slope and bed sediment characteristics at confluences produce markedly different upstream and downstream habitats that are exploited by different assemblages of macroinvertebrate larvae (Rice et al. 2001*a*, 2001*b*). The proportions of the net-spinning caddisfly *Arctopsyche* sp. (Hydropsychidae) and the filter-feeding caddisfly *Brachycentrus americanus* (Brachycentridae) increase downstream of confluences where large bed particles provide relatively stable substrates and shallow, high-velocity flows maximize seston supply, which suit their sessile feeding habits. Kiffney et al. (2006) report that confluences in three river basins in Washington State are associated with habitat discontinuities (nutrient loading, wood loading, substrate size, channel slope, water depth) and significant shifts in primary productivity (periphyton biomass), sculpin density (*Cottus* sp.), and the abundance of salmonids. Moreover, species richness, measured as species × size classes, peaked on the mainstream close to 7 of the 12 tributaries studied.

Our results indicate that the potential for biotic diversity due to this zonal effect should increase with aggradation driven by high FR×DR, and we therefore hypothesize that as the volume and grain sizes of the tributary bed load increase relative to the mainstream load, there will be increases in (hypothesis 1*a* (H1*a*)) the degree and extent of zonal (upstream versus downstream) habitat differentiation, (H1*b*) overall measures of biotic diversity around confluences, and (H1*c*) the dissimilarity of upstream and downstream communities. Our results also indicate that zonation produces lower Froude numbers and finer bed materials in upstream zones and higher Froude numbers and coarser bed materials in downstream zones. We therefore hypothesize that (H2*a*) the zones upstream and downstream from confluences are more likely to support assemblages of plants and animals that exhibit lentic and lotic characteristics, respectively, and (H2*b*) that this distinction will become more marked as FR×DR increases.

Our modeling also predicts strong environmental gradients within each zone, again driven by aggradation. This variability further enhances the range of available habitats and might further increase biodiversity at confluences by supporting longitudinal biotic gradients. We therefore hypothesize that as FR×DR increases (H3*a*) environmental and (H3*b*) biotic gradients become steeper (more change per unit distance) and extend over longer distances upstream and downstream from confluences. In the absence of appropriate physical and biological data, these seven hypotheses remain to be tested in the field.

Implications for network-scale understanding of biodiversity

Our modeling results reveal that increases in habitat heterogeneity at confluences are primarily controlled by relative bed load yield and relative bed load grain size so that the greater the value of FR×DR, the greater is the mainstream heterogeneity that is produced. This finding is important because it highlights the relative unimportance of flow characteristics and contrasting importance of sediment delivery and sediment characteristics for understanding tributary impacts. Consequently, our results emphasise the importance of identifying and quantifying the significant sediment sources and sediment routing pathways within the hydrological channel network, because it is these that may be most important for identifying key confluences and putative biological hot spots. However, hydrological and sedimentary networks are not necessarily related to one another in straightforward ways: basins that produce large amounts of water may not produce large amounts of sediment, and sediment characteristics, especially in headwater areas, may be unrelated to hydrological characteristics (Rice 1998).

By demonstrating the conditions under which tributaries produce a mainstream response and examining what controls the magnitude of that response, our numerical experiments have improved understanding of tributary-induced heterogeneity. They provide a rigorous foundation of testable relations upon which additional experimental and empirical work can further develop understanding of the spatial and temporal characteristics of tributary impacts at local, confluence-zone scale. If useful measures of the key independent variables could be defined (FR, DR, QR), either using surrogate measures or by other means, then these local-scale results could be used to develop network-scale models of in-stream habitat heterogeneity. By adding process-based understanding of tributary–mainstream interactions, our work therefore extends several recent advances in stream ecosystem theory, including the link discontinuity concept (Rice et al. 2001*a*) and the valuable framework provided by the network dynamics hypothesis (Benda et al. 2004*b*). More generally, our findings strengthen calls for a "fluvial landscape ecology" (Poole 2002; Wiens 2002; Fisher et al. 2004), which emphasises that rivers are spatially distributed, heterogeneous systems in which the shape and topology of the drainage network and the connections between tributaries and recipient channel segments are key controls of ecological functions and the distribution of lotic organisms (Osborne and Wiley 1992; Fagan 2002; Power and Dietrich 2002).

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Discharge and hydraulic interactions in contrasting channel morphologies and their influence on site utilization by spawning Atlantic salmon (*Salmo salar*)

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Abstract: Six study sites were selected to represent the range of channel morphologies, extending from dynamic pool–riffle to transitional step–pool/plane bed reach types, used by spawning Atlantic salmon (*Salmo salar*) in a small upland Scottish stream. The hydraulic functioning of reaches over the range of discharges used by spawning fish was characterized, and the influence of hydraulic heterogeneity and rates of change in discharge on the frequency of spawning was assessed. Relationships between discharge and depths and velocities differed significantly between sites; thus, hydraulic responses to changes in discharge were different. The range of discharges used for spawning differed between sites, although optimum discharges were similar. Integration of hydraulic information with microhabitat suitability predicted that spawning conditions should occur at discharges higher than those utilized by fish. There was no evidence that hydraulically heterogeneous sites were used more frequently than homogeneous ones. Rather, data suggest that the frequency of utilization of sites was governed principally by the availability of suitable sediment. Flow stability was important for spawning, with periods of rapidly varying discharge avoided. It is suggested that the rate of change in discharge should be considered more explicitly when assessing environmental flow needs.

Résumé : Nous avons choisi six sites d'étude pour représenter la gamme des morphologies des chenaux utilisés par les saumons atlantiques (*Salmo salar*) durant la fraye dans un petit cours d'eau des terres hautes d'Écosse; les types de fonds des sections varient de systèmes dynamiques à fosses–rapides à des systèmes de transition avec seuils–fosses/fonds plats. Nous avons caractérisé le fonctionnement hydraulique des sections sur toute l'étendue des débits utilisés par les poissons durant la fraye et nous avons évalué l'influence de l'hétérogénéité hydraulique et des taux de changement de débit sur la fréquence de la fraye. Il y a des différences significatives d'un site à l'autre dans les relations entre le débit et les profondeurs et les vitesses de courant; les réactions hydrauliques aux changements de débit sont donc variables. L'étendue des débits utilisés pour la fraye varient d'un site à un autre, bien que les débits optimaux soient semblables. L'intégration des données hydrauliques et de la convenance des microhabitats mène à des prédictions voulant que les conditions de fraye devraient se produire à des débits plus importants que ceux utilisés par les poissons. Il n'y a pas d'indication que les sites hétérogènes soient utilisés plus fréquemment que les sites homogènes. Au contraire, des données laissent croire que la fréquence d'utilisation des sites est contrôlée surtout par la disponibilité de sédiments adéquats. La stabilité de l'écoulement est important pour la fraye et les périodes de variations rapides du débit sont évitées. Nous croyons qu'on devrait tenir compte de façon plus explicite du taux de changement du débit dans la détermination des besoins d'écoulement dans le milieu.

[Traduit par la Rédaction]

Introduction

Knowledge of the interactions between river discharge, channel morphology, and channel hydraulics and how these interactions influence biological communities is required for instream habitats to be maintained and, where appropriate, enhanced or restored (Petts and Maddock 1996; Cowx and Welcome 1998). Instream physical habitat is most frequently characterized at the microscale by measurement or calculation of hydraulic conditions such as depth, velocity, shear stress, and Froude number. Many studies have assessed the links between these microscale conditions and species of fish (Heggenes 1990; Heggenes and Saltveit 1990; Moir et al. 2002) and invertebrates (Gibbins et al. 1996; Hastie et al.

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2000; Mérigoux and Dolédec 2004). Microscale hydraulic conditions are produced as a result of the interaction of discharge, channel morphology, and sedimentary characteristics; these interactions ultimately control the temporal and spatial distribution of suitable physical habitat for a particular species (Thompson et al. 2001).

A number of approaches have been used to describe and explain the relationships between discharge and habitat, many of which were initiated through concerns over salmonid populations in North America (Gordon et al. 2004). These have ranged in complexity and scale from assessments based on the historical flow record to define the minimum discharges that maintain a specified ecological status (e.g., the "Montana method" described by Tennant 1976) to integrated numerical habitat models of relatively small stream sections. The latter approaches are now the mainstay of ecological flow assessment (Reiser et al. 1989; Dunbar et al. 1998), the most widely employed approach being the Physical HABitat SIMulation (PHABSIM) system (Bovee 1982; Tharme 2003). Other more sophisticated habitat models that incorporate two-dimensional (2D) and three-dimensional (3D) hydraulic simulations have since been developed (Leclerc et al. 1995; Ghanem et al. 1996; Pasternack et al. 2004), although the methodologies are conceptually the same as in PHABSIM. Another group of procedures, termed "transect" or "hydraulic rating" methods (Tharme 2003), adopt principles of "at-a-station" hydraulic geometry (e.g., Collings et al. 1972; Hogan and Church 1989; Jowett 1998). These procedures characterize a site using a series of cross sections describing empirical relationships between discharge and channel hydraulics that are then related to species' instream habitat requirements in some way. Transect approaches are relatively simple to apply and have low data acquisition and processing requirements compared with habitat modelling (Tharme 2003). The output is typically given as reach or cross-section averages, a somewhat lower spatial resolution than reach-scale modelling approaches (Tharme 2003; Gordon et al. 2004).

Webb et al. (2001) and Gibbins et al. (2002) described an alternative approach to the assessment of instream flow requirements. They developed a method coupling direct observations of site selection by spawning Atlantic salmon (*Salmo salar*) with hydrological measurement to produce an index of discharge electivity. By assessing discharge use directly (i.e., rather than coupling a hydraulic model to habitat suitability indices (HSIs) to compute a discharge suitability function), they avoided many of the complexities associated with habitat modeling; in particular they avoided the problems of simulating highly non-uniform flow in the complex channel morphologies that typically exist in high-gradient upland streams (Moir et al. 2005).

These different approaches provide data at different resolutions and vary as to whether their links to stream ecology are explicit, implicit, or assumed. Salmonid fish have been an important focus of instream flow studies both because their size and behaviour lend themselves well to observations and measurement of habitat use and because of their economic, cultural, and recreational importance. There is now an extensive literature on the spawning microhabitat requirements of salmonids, particularly in relation to depth, velocity, and substrate (e.g., Beland et al. 1982; Crisp and Carling 1989; Moir et al. 1998). Although many authors have suggested that suitable microhabitats are associated with particular channel geomorphic characteristics (e.g., Payne and Lapointe 1997; Dauble and Geist 2000; Fukushima 2001), few have examined this relationship explicitly. Montgomery et al. (1999) showed that spawning of several Pacific salmonid species was preferentially located in pool–riffle channel morphologies. Similar findings were presented by Moir et al. (2004), who related over 800 individual observations of spawning activity by Atlantic salmon to channel morphology and stream discharge in two Scottish upland streams. They found that spawning occurred predominantly in "response" reach types (e.g., pool–riffle; see Channel morphological classification section for a description of the classification methodology) and less frequently in "transport" morphologies (e.g., plane bed, step–pool) and that the former reach types permitted spawning over a significantly greater range of flows. They hypothesized that the high morphological and hydraulic heterogeneity related to the bar sequences that characterize response reaches provided suitable microhabitat conditions for spawning over a greater discharge range; thus, as flows fluctuated over the spawning season, sections of the stream with response (i.e., pool–riffle) morphology provided a longer cumulative duration of suitable habitat conditions. Their results and hypotheses were consistent with the work of Mosely (1982), who demonstrated that braided channels characterized by a complex and dynamic bar morphology provided suitable habitat conditions for juvenile salmonids over a wider range of flows than simpler, single-thread channels. Furthermore, Webb et al. (2001) and Moir et al. (2004) found that there were broader, catchment-scale patterns to discharge use by spawning fish, e.g., the minimum discharge used by spawners increased with distance upstream. Webb et al. (2001) observed that individual Atlantic salmon spawning sites were utilized across specific flow ranges and that these ranges were consistent between spawning seasons. This suggested that the interaction of flow with the particular channel morphology of a site determined the range of discharges that provided suitable spawning conditions.

These studies represent some of the few that have attempted to link microhabitat conditions both to meso-scale morphological features and to stream discharge in order to understand the spatial and temporal influences on salmonid spawning. They identify important between-reach type and within-catchment differences in discharge use that would not be apparent in approaches such as PHABSIM, which tend to be restricted to single study sites because of cost and logistics. Such differences have important implications for how flow change or regulation might affect habitat suitability throughout a system; this in turn has implications for the allocation of environmental flows. It is important that the generality of such findings is assessed by undertaking similar studies in other catchments and that the mechanisms responsible for the observed, broad-scale patterns are investigated at finer resolution by undertaking process-based studies.

In this paper, we use a hydraulic rating approach to describe relationships between discharge and microhabitat conditions in contrasting channel morphologies utilized by spawning Atlantic salmon in an upland stream. The paper addresses five questions. (*i*) Do discharge – channel hydraulic (depth, velocity) relationships differ between reach types? (*ii*) Does the hydraulic heterogeneity of a reach influence the frequency of spawning there (total number of spawning incidents)? (*iii*) What is the relationship between hydraulic heterogeneity and discharge? (*iv*) Do direct observations of discharge use by spawning fish correspond to predictions of suitability based on the integration of hydraulic and sedimentary data with HSIs? (*v*) Does discharge instability influence spawning behaviour? This paper is based on field observations of spawning in three consecutive years in the Allt a' Ghlinne Bhig, Scotland, and surveyed hydraulic data for six sites distributed throughout the stream.

Materials and methods

Study area and sites

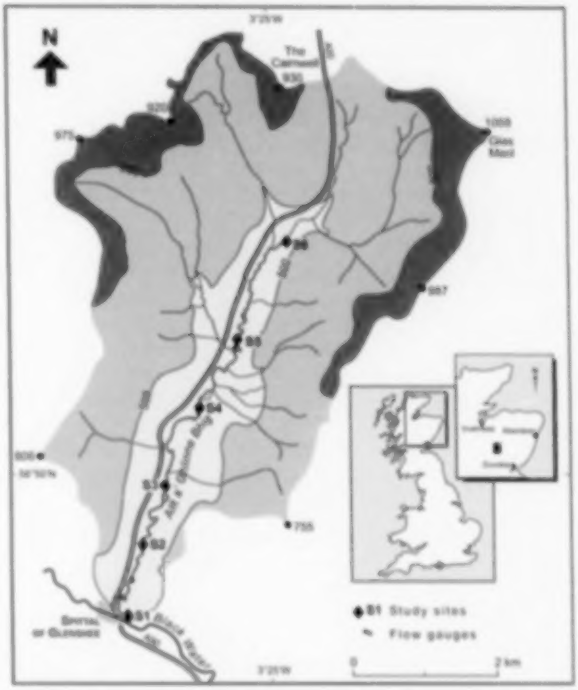
The Allt a' Ghlinne Bhig (Fig. 1) drains a catchment area of 27.5 km^2 and has a mean altitude of 641 m. The highest point in the catchment is the summit of Glas Maol at 1068 m. The stream rises at an altitude of approximately 800 m and flows 12 km in a generally southerly direction to join the Black Water at 335 m. The mean bed slope over the section of the stream accessible to salmon is 0.018 $m \cdot m^{-1}$, although at the reach scale (5–10 channel widths in length), this varies from 0.058 $m \cdot m^{-1}$ in the headwaters to 0.006 $m \cdot m^{-1}$ in the downstream sections. Median annual discharge gauged near the mouth of the stream is 0.87 $m^3 \cdot s^{-1}$. Surveys carried out in 2000–2002 showed that spawning occurred between 26 October and 16 November (Moir et al. 2004). Over this period, median flows were 1.37 $m^3 \cdot s^{-1}$ (2000), 1.16 $m^3 \cdot s^{-1}$ (2001), and 1.50 $m^3 \cdot s^{-1}$ (2002). However, there was much variation around these median discharge values, with coefficients of variation (based on 15-min data) of 130.6% (2000), 59.2% (2001), and 84.6% (2002).

Detailed observations of spawning activity (defined below) along the entire length of the Allt a' Ghlinne Bhig were made in 2000, 2001, and 2002 (Moir et al. 2004). These observations provided information on the location, discharge, and channel morphology associated with 423 incidences of spawning. These data guided the selection of the six sites where repeat hydraulic surveys were carried out for the present study (Figs. 1 and 2; Table 1). Site selection was based on three main criteria: (*i*) the sites were utilized by spawning salmon in all three observation years, (*ii*) together the sites were representative of the size and morphological characteristics exhibited by spawning reaches in the stream, and (*iii*) there was variation in the flow ranges used by spawning fish between sites. The longitudinal extent of each site was determined by the dimensions of the morphological unit (e.g., bar feature) across which spawning occurred.

Channel morphological classification

The entire length of the study stream was characterised using an adaptation of the classification methodology described by Montgomery and Buffington (1997). Their classification is process-based, reflecting the relative balance of reach-scale sediment transport vs supply processes. Where sediment supply exceeds transport capacity, reach types are classified as "response" (braided, wandering, and pool–riffle channels) and "transport" (bedrock, cascade, step–pool, and plane bed channels), where sediment supply is less than transport capacity. Particular reach types are characteristic of different points on the axis representing the ratio of sediment supply to transport capacity; thus reaches types represent a continuum from cascade – step–pool – plane bed – pool–riffle – wandering – braided channels (Fig. 3). In practice, some reaches exhibit morphological characteristics common to adjacent members of the sequence (e.g., plane bed and pool–riffle) and can be considered as being "transitional". In the present study, these transitional morphologies were classified in terms of the dominant and subdominant reach type, e.g., plane bed/pool–riffle if the channel exhibited morphological characteristics more in common with plane bed than pool–riffle. An additional reach type of dynamic pool–riffle was included in the sequence. This reach type was associated with dynamic bar sequences that provided a more heterogeneous topography than a typical pool–riffle channel but not sufficient to be classified as "wandering" (Ferguson and Werritty 1991) or "braided". It was therefore regarded as a transitional morphology between wandering and pool–riffle and hypothesised to represent the highest sediment supply to transport capacity ratio found in the study stream.

Fig. 1. The Allt a' Ghlinne Bhig watershed and study sites (Scotland, UK).



Topographical heterogeneity is implicit within the channel geomorphic classification system of Montgomery and Buffington (1997). Plane bed reaches are associated with minimum morphological variability as, by definition, they are characterised by a lack of distinctive bedforms that are the dominant control on topographical heterogeneity within channels (Montgomery and Buffington 1997). Morphological variability increases in channels with a higher or lower

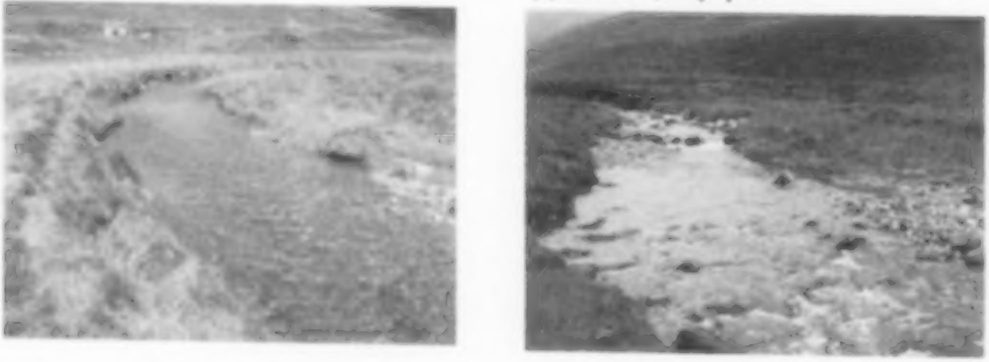
Fig. 2. Photographs of the six study sites. Reach type classifications (refer to Fig. 3): d p-r, dynamic pool–riffle; p-r, pool–riffle; p-r/pb, transitional pool–riffle/plane bed (pool–riffle dominant); pb/p-r, transitional plane bed/pool–riffle (plane bed dominant); pb, plane bed; s-p/pb, transitional step–pool/plane bed (step–pool dominant).

(a) Site 1, d p-r

(b) Site 2, pb/p-r

(c) Site 3, p-r

(d) Site 4, d p-r



(e) Site 5, p-r/pb

(f) Site 6, s-p/pb

sediment supply to transport capacity ratio as a result of the characteristic bedforms associated with these reach types (boulder steps in step–pool channels, bar features in pool–riffle sections).

Spawning observation

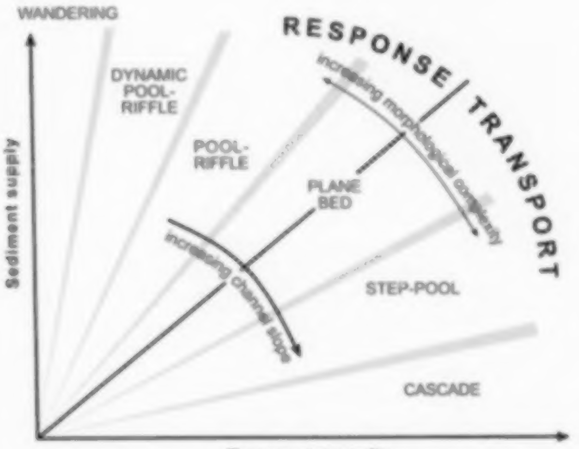
In each study season, observation surveys began on the commencement of spawning activity and continued until only sporadic incidents were detected, typically after 2 to 3 weeks (Moir et al. 2004). On each day when a survey was undertaken, the length of the stream from the confluence with the Black Water to the upstream limit of spawning (a waterfall impassable to fish 9 km upstream) was walked in daylight hours (0800 to 1600) (Fig. 1). A total of 49 days was spent walking the stream over the three study seasons (15 in 2000, 20 in 2001, and 14 in 2002). There was a total

Table 1. Study site characteristics.

Characteristic	Study site 1	2	3	4	5	6
Catchment area at site (km^2)	27.5	25.8	24	20.5	11.7	6.8
Distance upstream (km)	0.1	1.8	2.7	4.6	5.9	7.9
Median discharge (Q_{50}) (m^3·s^{-1})	0.87	0.82	0.76	0.66	0.38	0.22
Slope (m·m^{-1})	0.0074	0.0062	0.0081	0.0107	0.0074	0.0446
Bankfull width (m)	12.2	8.3	9.6	10.3	5.1	5.9
Mean bankfull depth (m)	0.94	1.38	1.02	0.97	0.86	0.57
D_{50} (mm)	42.2	46.9	41.1	54.2	25.8	77.7
Area of site (m^2)	675	553	247	197	122	79
Area of spawning substrate (m^2)	643	450	227	152	117	44
Channel morphology	d p-r	pb/p-r	p-r	d p-r	p-r/pb	s-p/pb
Spawning flows (Q_t) (m^3·s^{-1})	1.0–2.8	0.9–2.7	0.9–2.1	1.0–1.6	1.2–2.1	1.5–3.0
Mean Q_t (m^3·s^{-1})	1.44	1.43	1.39	1.31	1.57	2.04
No. spawning observations	41	28	36	10	9	6
Spawning·m^{-2} (whole site)	0.061	0.051	0.146	0.051	0.074	0.076
Spawning·m^{-2} (suitable sediment)	0.064	0.062	0.159	0.066	0.077	0.136

Note: Channel morphology classifications (refer to Fig. 3): d p-r, dynamic pool–riffle; p-r, pool–riffle; p-r/pb, transitional pool–riffle/plane bed (pool–riffle dominant); pb/p-r, transitional plane bed/pool–riffle (plane bed dominant); pb, plane bed; s-p/pb, transitional step–pool/plane bed (step–pool dominant).

Fig. 3. Schematic representation of the physical controls on the typical channel morphologies in upland Scottish streams (modified from Montgomery and Buffington (1997) and Moir et al. (2004)).



of only 4 days when surveys were not carried out because of adverse weather or high flow conditions. Polarized sunglasses were worn to aid in the observation of spawning activity. Clear observation of the channel was possible up to flows of approximately 7 times median flow (i.e., approximately 6 m^3·s^{-1} as measured at the downstream flow gauge). The highest flow at which spawning was observed to occur at any of the study sites was 3.0 times median flow (site 6). Therefore, high flows are unlikely to have obscured observation of spawning activity and biased results at the study sites. During the surveys, the location and time that each female fish was observed spawning was logged. Spawning (initial cutting and oviposition) was defined using the classification of Jones (1959). The location of spawning sites was determined using a handheld global positioning system (GPS; model Garmin GPS 12XL; Garmin Ltd., Olathe, Kansas). Data were translated to distance upstream from the Black Water confluence. In total, 423 spawning observations were logged, with each mapped and indexed to channel morphology and, as detailed below, discharge at the time of spawning. Because of the inherent accuracy of the GPS unit, all observations were assigned only to a particular study site, not to a point within the site.

Discharge assessment

A stage recorder was installed 0.5 km upstream from the Black Water confluence and a stage–discharge relationship was determined from 13 gaugings (0.30–4.6 m^3·s^{-1}). Before the 2001 and 2002 study seasons, further gaugings had been made to allow assessment of any adjustment of the stage–discharge relationship as a result of morphological changes at the site. However, no such adjustment was observed. Data from this site and comparison with three nearby, long-term gauged streams (River Ardle at Kindrogan, River Isla at Forfar, and River Ericht at Craighall; Scottish Environmental Protection Agency (SEPA), Perth, Scotland; 15-min interval data) provided a longer-term estimate of the annual median discharge at the Allt a' Ghlinne Bhig. This was done by calculating ratios of the median flow over the measured period at the Allt a' Ghlinne Bhig to the equivalent values from the SEPA gauges. The ratios were then applied to the annual median flow statistics for the three SEPA-gauged streams to give an estimate of the long-term annual median discharge at the Allt a' Ghlinne Bhig. This procedure yielded a long-term median discharge (Q_{50}) of 0.87 m^3·s^{-1} for the Allt a' Ghlinne Bhig gauge site.

Although spot discharge measurements were made at each of the study sites for each hydraulic survey (described below), continuous discharge data for any position within the stream had to be calculated from the data obtained at the downstream gauge (Fig. 1). To calculate an instantaneous discharge at a specific location within the stream, the flow data from the downstream gauging site were adjusted according to catchment area and mean altitude using empirical relationships developed by Wade (1999) for nearby mountain streams:

$$Q_u = Q_g\left[\left(\frac{\mathrm{CA}_u}{\mathrm{CA}_g}\right)\left(\frac{P_u}{P_g}\right)\right]$$

where Q is discharge, the subscripts u and g refer to ungauged (i.e., a specific location within the stream) and gauged (i.e., at the downstream gauge), respectively, and CA is catchment area. P is mean annual precipitation in millimetres and is estimated from the empirical relationship (derived for upland streams in the Cairngorm mountains, close to the study stream):

$$P = 1.27\mathrm{ALT} + 501$$

where ALT is the mean altitude of the catchment upstream from that particular location on the stream. Using this equation, the mean annual precipitation for the entire Allt a' Ghlinne Bhig catchment is estimated at 1197 mm, very close to that measured at a nearby weather station (1143 mm).

For the nearby Girnock Burn, Gibbins et al. (2002) assessed the error associated with site discharges calculated using these equations and showed that calculated and measured discharges differed by between 3% (low flows) and 7% (high flows). The discharge gaugings carried out at each of the hydraulic surveys (detailed below) were used to generate a second estimate of error. Of the 46 data pairs (the total number of gaugings carried out at the six study sites), predicted discharge using the method described above ranged from −7.7% to +12.1% of that measured, with a mean difference of +3.1%. On the basis of these data, it was concluded that the method used to predict site-specific discharge was acceptable. To allow comparison of data between specific locations within the study stream, instantaneous site-specific discharge was normalized by respective site median values (i.e., Q_{50}) to produce a discharge index, Q_r (Webb et al. 2001; Gibbins et al. 2002); hence, Q_r is simply the instantaneous discharge at a specific location in the stream expressed relative to the median discharge for that location.

The instantaneous discharge recorded at the downstream gauge may not match that at other locations in the stream at the same point in time, particularly given the flashy nature of the Allt a' Ghlinne Bhig. As an extreme example, the passing of a flood wave through the system would result in markedly different discharges at a given point in time. To account for lag times between the gauge and other locations on the stream, a simple temporal correction was applied to the discharge time series. During the 2000 spawning season, a second-stage recorder was temporarily installed at a site in the upper catchment, approximately 5 km upstream from the lower gauge (Fig. 1). The data from this station provided information on the transmission times of flows through the system. By comparing the time that specific flow events (i.e., flow peaks) occurred at the two sites, mean propagation velocity through the system could be calculated. Nine separate flow events (flow peaks ranging from 2.4 to 9.7 Q_r as measured at the downstream gauge) were identified that could be matched between the two sites during the period when both stage recorders were operational (15 October – 25 November 2000). The transmission time of these nine events varied from 1 h 45 min to 2 h 15 min (flow data were recorded at 15-min intervals at both locations) with a mean of 2 h 11 min. From these data and the known distance between the two gauging stations, mean propagation velocity was calculated. The distance between the gauging site and any spawning location was determined from the longitudinal stream position database. This distance and the mean propagation velocity permitted an estimate of the lag time between the two locations; this correction was applied to the 15-min interval time series data to estimate Q_r at a specific spawning location at the time that spawning was observed.

Discharge electivity index

The method described by Gibbins et al. (2002) to produce a discharge electivity index was also applied in this study. This index discriminates between selection and avoidance, in this case of relative discharge (Q_r) classes. Frequency distributions of discharges used by and available to fish were constructed for the 2000–2002 spawning seasons. From these data, the "relativized electivity index" was produced (Vanderploeg and Scavia 1979; Lechowicz 1982):

$$E^* = \frac{\left(\frac{R}{\sum R}\right) - \frac{1}{n}}{\left(\frac{R}{\sum R}\right) + \frac{1}{n}}$$

where R is the ratio of the proportions of utilization to availability in each Q_r class interval and n is the number of class intervals. E^* varies between −1 (avoidance) and +1 (selection) with 0 representing indifference. Discharge electivity was calculated using all spawning observation data obtained throughout the stream in the 2000–2002 study seasons.

Hydraulic characterization

Each study site was characterized by between five and seven transects, with three to six measurement points across each transect (Table 2). The total number of measurement points per site was governed by the longitudinal and lateral size of the site and its morphological complexity; more data points were necessary in larger and more complex sites. Measurement points were the same over successive hydraulic surveys. The measurement points were selected to representatively characterize the physical heterogeneity of each study site and were therefore not evenly distributed. At each of these points, measurements of depth and velocity were taken over a range of discharges. Because of the flashy hydrological regime of the Allt a' Ghlinne Bhig, hydraulic surveys had to be carried out within a 30-min period to minimize the potential bias due to flow variation, especially during higher flows. Hence, although more data points would have been preferable for site characterization, this would have increased survey time and potentially introduced bias associated with flow change. Repeat surveys were carried

Table 2. Study site hydraulic survey information.

Site	No. of transects	No. of survey points	No. of surveys	Surveyed flows (Q_i)	Surveyed flow duration range
1	6	26	7	0.38, 0.75, 0.87, 1.14, 1.85, 2.69, 3.80	Q_{95}–Q_7
2	7	35	7	0.50, 0.76, 0.98, 1.25, 1.78, 2.52, 3.08	Q_{88}–Q_{10}
3	5	20	7	0.40, 0.71, 1.00, 1.25, 1.76, 2.52, 3.31	Q_{94}–Q_9
4	5	24	8	0.40, 0.70, 0.98, 1.26, 1.35, 1.76, 2.57, 3.32	Q_{94}–Q_9
5	6	18	9	0.46, 0.76, 0.97, 1.25, 1.36, 1.89, 2.52, 3.78, 5.45	Q_{91}–Q_4
6	5	16	6	0.40, 0.96, 1.25, 1.95, 2.97, 5.25	Q_{94}–Q_5

out at six to nine different discharges at each site between October 2002 and November 2003 (Table 2). Instantaneous discharge was measured at a suitable cross section at each site immediately before and after every hydraulic survey. If flows varied by more that 20% between the pre- and post-survey gaugings, the hydraulic survey data were discarded.

Depth and velocity were measured using a ranging pole and a Valeport electromagnetic velocity meter (Valeport Ltd., St. Peter's Quay, Totnes, Devon, UK), respectively. Mean water column velocity was measured at each survey point (0.6 × flow depth from the water surface) averaged over a 30-s interval. Ideally, velocity would have been measured at more positions within the water column (e.g., 0.2 and 0.8 × depth) to provide a better indication of mean column velocity (Byrd et al. 2000) and to characterize near-bed conditions experienced by spawning fish. However, this would have added considerably to survey times which, as discussed above, were problematic because of potentially rapidly changing flows in the Allt a' Ghlinne Bhig. During certain low-flow hydraulic surveys, some survey points became exposed, especially at channel margin locations in study sites exhibiting high topographical variability. These points were assigned depth and velocity values of zero.

Sediment character at each hydraulic survey point was visually assessed to determine its suitability for spawning. This assessment was based on the criterion that to permit spawning, a location should have the proportion of material >64 mm intermediate axis diameter (i.e., cobbles and boulders) less than 25% frequency (Moir et al. 2002).

For each study site and discharge, the 5th, 25th, 50th, 75th, and 95th percentile values were determined for the depth and velocity measurements. The use of these percentiles provided a method of describing hydraulic variability at each study site that was not biased by extreme values. At-a-station hydraulic geometry-type relationships were constructed for all of the depth and velocity distribution descriptors (i.e., the 5th, 25th, 50th, 75th, and 95th percentiles), and trend lines were fitted to each. Unlike conventional hydraulic geometry approaches, these were not necessarily power functions; logarithmic functions were used if they provided a better fit to the data. The hydraulic conditions at the time of spawning activity at a site were estimated by substituting individual spawning observation discharges into these functions.

Spawning microhabitat suitability data

Information on the microhabitat requirements of spawning Atlantic salmon was available from data obtained in three similarly sized upland tributaries in the adjacent River Dee catchment (Moir et al. 2002). These data were used to produce HSIs. Rather than using continuous suitability curves, simple "binary" criteria were produced, defined by the a priori limits of substrate, water depth, and velocity use known for spawning fish. Water depth over suitable substrate must be at least 0.125 m, the minimum useable depth for Atlantic salmon (Moir et al. 2002; Armstrong et al. 2003). Then, the combination of depth and velocity must satisfy the condition $0.2 \le \mathrm{Fr} \le 0.75$ for habitat to be considered suitable, where Fr is the Froude number:

$$\mathrm{Fr} = \frac{v}{\sqrt{dg}}$$

where v is velocity, d is depth, and g is gravitational acceleration ($9.81\ \mathrm{m^2 \cdot s^{-1}}$). The Froude number was shown by Moir et al. (2002) to provide a means to account for the interdependence of depth and velocity observed in the microhabitats utilized by spawning salmonids. Its dimensionless nature also permits comparison between sites that differ in size. The sediment HSI was as defined in the section above.

Discharge vs habitat availability curves, similar to those produced by PHABSIM, were produced for each site by applying the HSIs to the point hydraulic and sedimentary data obtained at each of the surveyed discharges. Suitability was calculated for each survey point at each site at each discharge. If the a priori criteria at a particular survey point were not met, it was considered unsuitable. For any given discharge, the proportion of survey points with suitable conditions was calculated in order to give a measure of site suitability. The flow ranges over which these values were calculated are given in Table 2, expressed in terms of Q_i and flow-duration percentiles.

Results

Relationships between discharge and site hydraulics

The relationships between the discharge index (Q_i) and the distributions of depth and velocity at the six study sites are shown (Fig. 4); equations for the fitted lines are also provided (Table 3). The plots essentially describe the "hydraulic domain" across the surveyed range of flows at each of the study sites, the 5th and 95th percentile best-fit curves defining the central 90% of depths and velocities available to fish. All of the 60 possible relationships (i.e., the 5th, 25th, 50th, 75th, and 95th percentile relationships for depth and velocity at each of the six study sites) proved significant ($P < 0.001$). Power functions proved the most appropriate fit to the data

Fig. 4. Hydraulic survey data for the six study sites. Fitted lines represent 5th, 25th, 50th, 75th, and 95th percentile values of survey data (▲, 5th; ▼, 95th; +, 50th; ◆, 25th and 75th). Reach type classifications (refer to Fig. 3): d p-r, dynamic pool–riffle; p-r, pool–riffle; p-r/pb, transitional pool–riffle/plane bed (pool–riffle dominant); pb/p-r, transitional plane bed/pool–riffle (plane bed dominant); pb, plane bed; s-p/pb, transitional step-pool/plane bed (step-pool dominant).

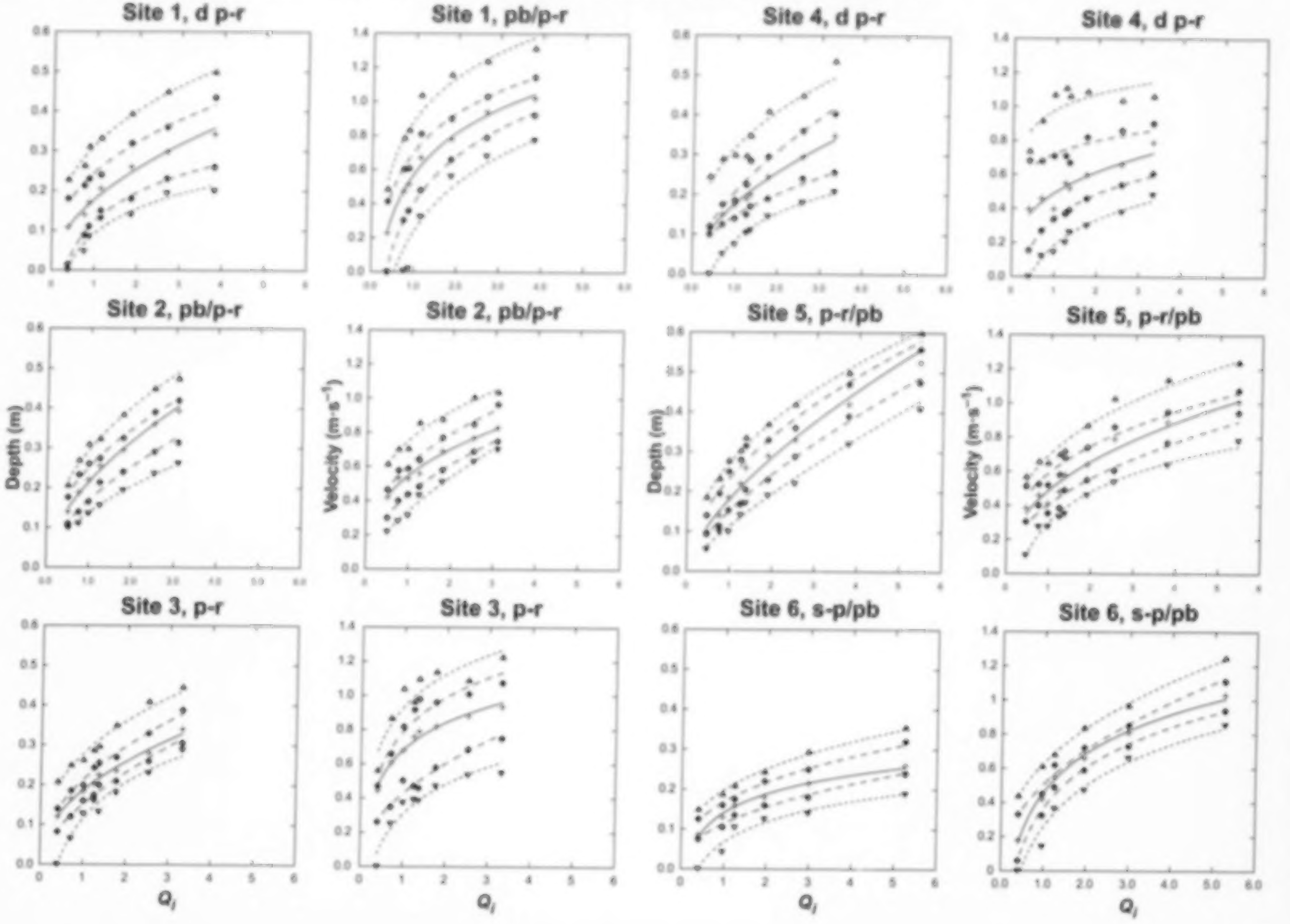


Table 3. Equations describing "best-fit" trend lines through empirical Q_i vs depth (d) and velocity (v) data at each of the study sites.

Site 1	
$d_5 = 0.315Q_i^{0.351}$, $R^2 = 0.994$	$v_5 = 0.894 + 0.832\log Q_i$, $R^2 = 0.982$
$d_{25} = 0.246Q_i^{0.392}$, $R^2 = 0.991$	$v_{25} = 0.709 + 0.745\log Q_i$, $R^2 = 0.991$
$d_{50} = 0.179Q_i^{0.520}$, $R^2 = 0.991$	$v_{50} = 0.578 + 0.800\log Q_i$, $R^2 = 0.996$
$d_{75} = 0.122 + 0.244\log Q_i$, $R^2 = 0.996$	$v_{75} = 0.408 + 0.909\log Q_i$, $R^2 = 0.999$
$d_{95} = 0.092 + 0.209\log Q_i$, $R^2 = 0.978$	$v_{95} = 0.242 + 0.921\log Q_i$, $R^2 = 0.946$
Site 2	
$d_5 = 0.297Q_i^{0.445}$, $R^2 = 0.994$	$v_5 = 0.756Q_i^{0.299}$, $R^2 = 0.982$
$d_{25} = 0.253Q_i^{0.460}$, $R^2 = 0.996$	$v_{25} = 0.609Q_i^{0.384}$, $R^2 = 0.992$
$d_{50} = 0.216Q_i^{0.557}$, $R^2 = 0.997$	$v_{50} = 0.549Q_i^{0.363}$, $R^2 = 0.988$
$d_{75} = 0.169Q_i^{0.509}$, $R^2 = 0.991$	$v_{75} = 0.437Qi^{0.491}$, $R^2 = 0.998$
$d_{95} = 0.138Q_i^{0.561}$, $R^2 = 0.998$	$v_{95} = 0.341Q_i^{0.664}$, $R^2 = 0.994$
Site 3	
$d_5 = 0.279Q_i^{0.372}$, $R^2 = 0.988$	$v_5 = 0.952 + 0.700\log Q_i$, $R^2 = 0.949$
$d_{25} = 0.214Q_i^{0.477}$, $R^2 = 0.995$	$v_{25} = 0.792 + 0.659\log Q_i$, $R^2 = 0.956$
$d_{50} = 0.187Q_i^{0.471}$, $R^2 = 0.994$	$v_{50} = 0.684 + 0.530\log Q_i$, $R^2 = 0.990$
$d_{75} = 0.151Q_i^{0.614}$, $R^2 = 0.993$	$v_{75} = 0.429Q_i^{0.496}$, $R^2 = 0.977$
$d_{95} = 0.116 + 0.302\log Q_i$, $R^2 = 0.988$	$v_{95} = 0.307 + 0.580\log Q_i$, $R^2 = 0.963$
Site 4	
$d_5 = 0.319Q_i^{0.365}$, $R^2 = 0.963$	$v_5 = 0.979 + 0.316\log Q_i$, $R^2 = 0.756$
$d_{25} = 0.207Q_i^{0.584}$, $R^2 = 0.983$	$v_{25} = 0.723Q_i^{0.146}$, $R^2 = 0.867$
$d_{50} = 0.177Q_i^{0.538}$, $R^2 = 0.997$	$v_{50} = 0.492Q_i^{0.325}$, $R^2 = 0.943$
$d_{75} = 0.146Q_i^{0.463}$, $R^2 = 0.991$	$v_{75} = 0.340 + 0.486\log Q_i$, $R^2 = 0.997$
$d_{95} = 0.084 + 0.228\log Q_i$, $R^2 = 0.997$	$v_{95} = 0.182 + 0.508\log Q_i$, $R^2 = 0.987$
Site 5	
$d_5 = 0.274Q_i^{0.467}$, $R^2 = 0.998$	$v_5 = 0.699Q_i^{0.343}$, $R^2 = 0.983$
$d_{25} = 0.235Q_i^{0.531}$, $R^2 = 0.989$	$v_{25} = 0.593Q_i^{0.343}$, $R^2 = 0.979$
$d_{50} = 0.182Q_i^{0.661}$, $R^2 = 0.992$	$v_{50} = 0.490Q_i^{0.430}$, $R^2 = 0.981$
$d_{75} = 0.152Q_i^{0.697}$, $R^2 = 0.997$	$v_{75} = 0.407Q_i^{0.462}$, $R^2 = 0.983$
$d_{95} = 0.113Q_i^{0.786}$, $R^2 = 0.994$	$v_{95} = 0.300 + 0.605\log Q_i$, $R^2 = 0.992$
Site 6	
$d_5 = 0.198Q_i^{0.345}$, $R^2 = 0.997$	$v_5 = 0.632Q_i^{0.406}$, $R^2 = 0.999$
$d_{25} = 0.168Q_i^{0.371}$, $R^2 = 0.996$	$v_{25} = 0.508Q_i^{0.480}$, $R^2 = 0.992$
$d_{50} = 0.141 + 0.157\log Q_i$, $R^2 = 0.995$	$v_{50} = 0.461 + 0.758\log Q_i$, $R^2 = 0.997$
$d_{75} = 0.114Q_i^{0.452}$, $R^2 = 0.994$	$v_{75} = 0.370 + 0.785\log Q_i$, $R^2 = 0.997$
$d_{95} = 0.067 + 0.170\log Q_i$, $R^2 = 0.977$	$v_{95} = 0.260 + 0.798\log Q_i$, $R^2 = 0.984$

Note: The 5, 25, 50, 75, and 95 subscripts denote the percentile values of the hydraulic distributions that together characterise the variability in depth and velocity at a specific flow.

in most cases (38 out of 60), with logarithmic relationships best describing the remaining significant trends. Over the same range of relative discharges, the range of depths and velocities enveloped within 5th to 95th percentile values was greater at some sites than others (Fig. 4), i.e., hydraulically, some reaches were more variable than others. This was further evident when the coefficients of variation of depth and velocity were plotted across the range of surveyed flows (Fig. 5); it can also be seen how hydraulic variation generally decreases with discharge in each reach type.

Analysis of covariance (ANCOVA) was used to test for differences in the slopes and intercepts of the lines fitted through the Q_i vs 50th percentile depth and velocity data (Table 4). Overall, the ANCOVA results indicate appreciable variation in the Q_i vs hydraulic relationships and, thus, the hydraulic functioning of the sites. Eight of the 15 comparisons (53%) of Q_i vs depth slopes indicated significant differences between sites, whereas 10 of the 15 intercepts (67%) differed significantly between sites ($P < 0.05$). Similar differences were found between site Q_i vs velocity relationships: 60% of slopes differed between sites, whereas 73% of intercepts differed. In some cases, the slopes differed between sites but the intercepts did not (e.g., velocity at sites 1 and 2) and vice versa (e.g., depth at sites 1 and 2).

Fig. 5. Coefficients of variation (CV; as an index of hydraulic variability) for depth and velocity over the surveyed flows at the six study sites. Reach type classifications (refer to Fig. 3): d p-r, dynamic pool–riffle; p-r, pool–riffle; p-r/pb, transitional pool–riffle/plane bed (pool–riffle dominant); pb/p-r, transitional plane bed/pool–riffle (plane bed dominant); pb, plane bed; s-p/pb, transitional step–pool/plane bed (step–pool dominant).

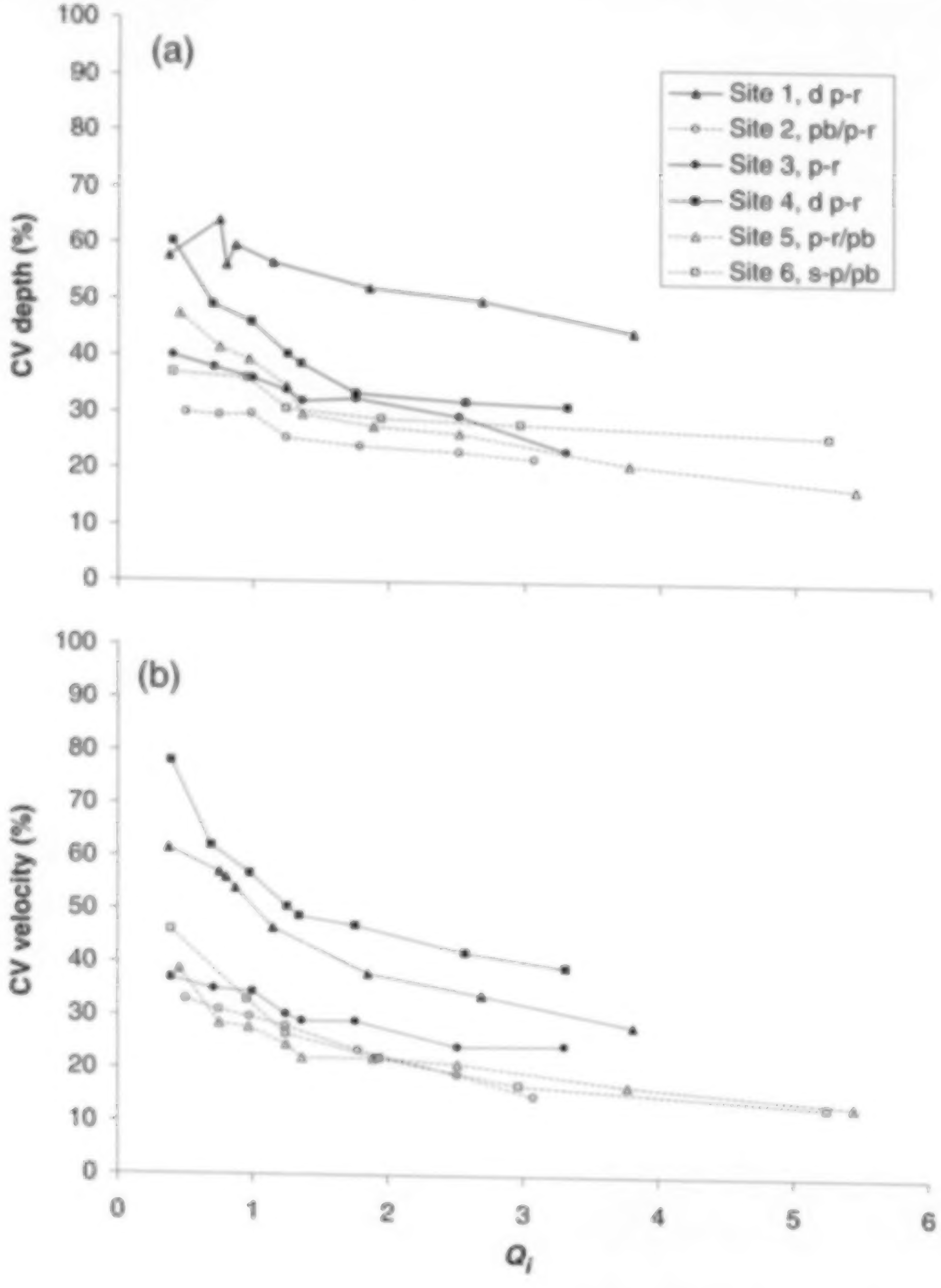


Table 4. Results of analysis of covariance (ANCOVA) tests comparing discharge index (Q_i) and (*a*) depth and (*b*) velocity relationships between study site pairings.

	Site				
Site	2	3	4	5	6
(a) Depth					
1	**I: $P = 7.20 \times 10^{-5}$** S: $P = 0.388$	I: $P = 0.169$ S: $P = 0.1714$	I: $P = 0.741$ S: $P = 0.630$	I: $P = 0.790$ **S: $P = 0.033$**	**I: $P = 2.24 \times 10^{-5}$** S: $P = 0.076$
2	n/a	**I: $P = 4.21 \times 10^{-5}$** **S: $P = 0.016$**	**I: $P = 6.06 \times 10^{-7}$** S: $P = 0.525$	**I: $P = 0.0011$** S: $P = 0.119$	**I: $P = 4.54 \times 10^{-6}$** **S: $P = 0.0091$**
3	n/a	n/a	**I: $P = 0.028$** **S: $P = 0.026$**	I: $P = 0.452$ **S: $P = 0.0029$**	**I: $P = 4.66 \times 10^{-7}$** S: $P = 0.468$
4	n/a	n/a	n/a	I: $P = 0.587$ **S: $P = 0.041$**	**I: $P = 8.81 \times 10^{-7}$** **S: $P = 0.010$**
5	n/a	n/a	n/a	n/a	**I: $P = 5.70 \times 10^{-5}$** **S: $P = 0.0019$**
(b) Velocity					
1	I: $P = 0.380$ **S: $P = 0.0178$**	**I: $P = 0.0029$** **S: $P = 0.0064$**	I: $P = 0.783$ **S: $P = 0.0026$**	I: $P = 0.437$ **S: $P = 0.041$**	**I: $P = 0.019$** S: $P = 0.691$
2	n/a	**I: $P = 0.0004$** S: $P = 0.467$	**I: $P = 0.014$** S: $P = 0.175$	**I: $P = 0.025$** S: $P = 0.287$	**I: $P = 0.0011$** **S: $P = 0.0078$**
3	n/a	n/a	**I: $P = 6.17 \times 10^{-6}$** S: $P = 0.782$	**I: $P = 2.64 \times 10^{-6}$** S: $P = 0.105$	**I: $P = 2.53 \times 10^{-5}$** **S: $P = 0.0028$**
4	n/a	n/a	n/a	I: $P = 0.377$ **S: $P = 0.040$**	**I: $P = 0.0027$** **S: $P = 0.0011$**
5	n/a	n/a	n/a	n/a	**I: $P = 0.014$** **S: $P = 0.015$**

Note: I refers to comparison of intercepts and S to slopes. Entries in bold show statistically significant differences ($P < 0.05$). n/a, not applicable.

Table 5. Multiple regressions statistics for analysis of the influence of sedimentary and hydraulic variables on the numbers of spawning fish using study reaches.

Multiple *R*	0.9	
Significance	0.030	
F	595	
df	regression 4, residual 1, total 5	
X variable	*t* stat	*P*
Area of suitable sediment	26	0.024
50th percentile depth	3.6	0.17
50th percentile velocity	6.7	0.09
CV velocity	3.6	0.17

Also, the slope of the relationship between Q_i and depth differed significantly between some sites, whereas that for Q_i vs velocity did not. Site 6, the most upstream site (a transitional step–pool/plane bed reach type), was the most consistently different to the other sites, both in terms of the slopes and intercepts of discharge vs depth and discharge vs velocity relationships.

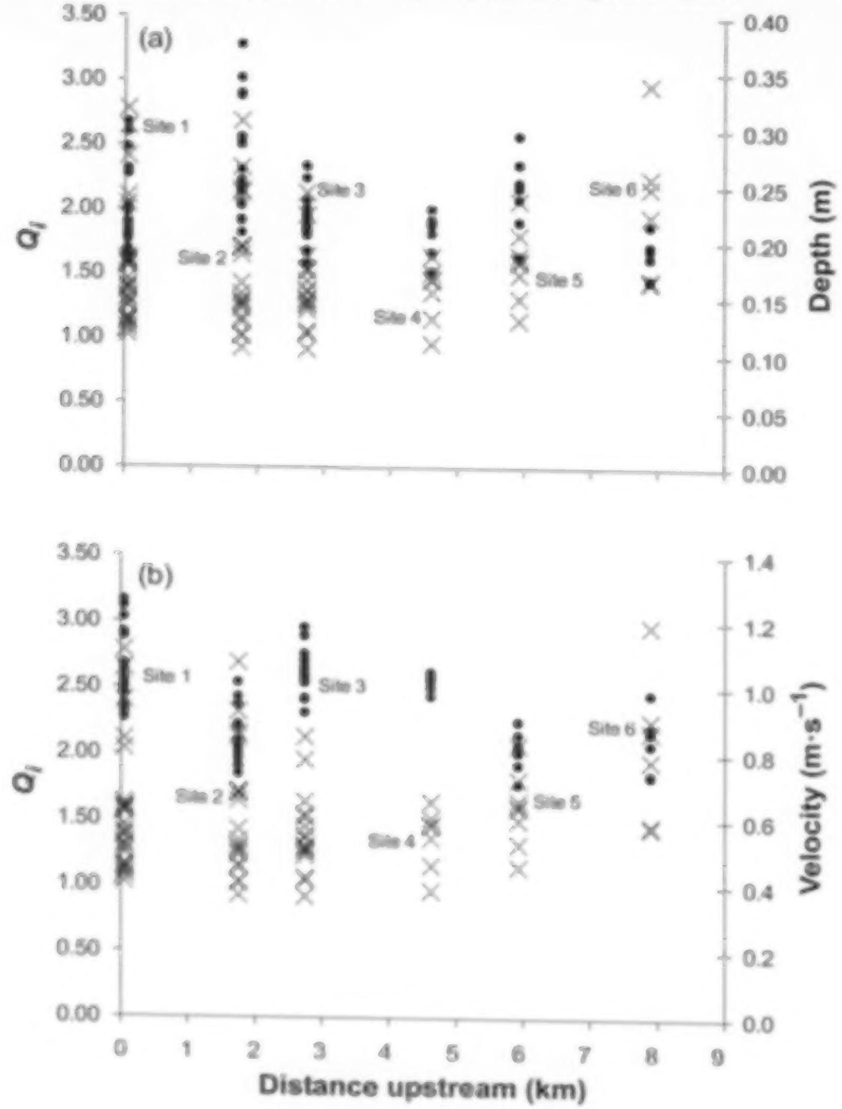
Site hydraulic characteristics and their utilization by spawning fish

Between-site differences in the number of spawning observations could be explained by a combination of the area of suitable sediment at respective sites, the coefficient of variation of velocity, and the 50 percentile depth and velocity values (multiple regression: df = 5, $F = 595$, $P = 0.034$; Table 5). Only the area of suitable sediment exerted a significant influence ($P = 0.024$) on the numbers of fish using respective sites, with the other variables individually not helping to explain a significant amount of the remaining variability.

Hydraulic controls on the limits of site utilization by fish

The relative discharges used by spawning fish at the six sites are plotted (Fig. 6), along with associated depth and velocity values (obtained using the empirical Q_i – hydraulic relationships; Table 3). There was considerable variation in the range of discharges utilized at the sites: site 2 (plane bed/pool–riffle) was used over a Q_i range of 0.92 to 2.69 (mean = 1.77), whereas site 4 (dynamic pool–riffle) was used over the range of 0.96 to 1.64 (mean = 0.66). The differences in ranges between sites resulted from differences both in the upper and lower limits to Q_i utilization. Although there appears to be no consistent spatial (along-stream) pattern to changes in the upper Q_i limits to spawning, the lower limits appear either to be constant (sites 1–4) or to increase with distance upstream (sites 4–6). Between-site differences in the ranges and means of Q_i utilization by spawning fish were tested using *F* tests and *t* tests, respectively (Table 6). Five of the 15 site pairings exhibited significantly different ($P < 0.05$) ranges of Q_i utilization; site 3 (pool–riffle) had a significantly lower Q_i range than sites 1 (dynamic pool–riffle), 2, and 6 (step–pool/plane bed), and site 6 had significantly lower range than sites 3, 4, and 5 (pool–riffle/plane bed). Site 6 had significantly greater mean Q_i utilization

Fig. 6. Comparison of distributions of Q_i and predicted hydraulic conditions associated with spawning observations at the study sites: ×, Q_i utilization; ●, site median (*a*) depth and (*b*) velocity obtained using regressions given in Table 3.



than the other five sites; the only other pairing with a statistical difference in mean Q_i use was with sites 4 and 5.

Q_i – available habitat relationships

The proportion of survey points predicted to support suitable microhabitat conditions for spawning is shown across the Q_i range (Fig. 7). Other than site 4, patterns were broadly similar at the sites, with rapidly increasing suitable habitat area up to ~2 × Q_i, then a more gradual decline. There was marked variation in the proportion of points providing suitable spawning habitat at each site at the median flow (i.e., Q_i = 1). At Q_i = 1, site 4 (dynamic pool–riffle) had 16% of the survey points suitable, compared with 66% at site 2 (plane bed/pool–riffle). The highest proportion of survey points predicted as being suitable (83%) was in the pool–riffle/plane bed channel of site 5 at a Q_i value of 2; at this discharge, only 45% of the survey points in the dynamic pool–riffle site (site 4) were predicted to support suitable microhabitat conditions. The observed incidents of spawning included in Fig. 7 indicate that Q_i values greater than 3 were not utilized at any of the sites. This conflicts with values of suitability predicted by integrating point hydraulic and sedimentary data with the HSIs, an integration suggesting that more than 50% of site survey points still have suitable microhabitat conditions at discharges in the 3–5 × Q_i range. The suitability of the sites for spawning (values of percent-

Table 6. Tests results for between-site differences in (*a*) the ranges (*F* test) and (*b*) the means (*t* test) of Q_i utilization by spawning fish.

	Site				
Site	2	3	4	5	6
(a) Depth					
1	$F = 1.25$ $F_c = 1.78$ $P = 0.260$	**$F = 2.20$** **$F_c = 1.99$** **$P = 0.030$**	$F = 2.62$ $F_c = 3.34$ $P = 0.092$	$F = 2.06$ $F_c = 3.04$ $P = 0.140$	$F = 1.88$ $F_c = 2.45$ $P = 0.119$
2	n/a	**$F = 2.75$** **$F_c = 2.07$** **$P = 0.012$**	$F = 3.28$ $F_c = 3.40$ $P = 0.055$	$F = 2.58$ $F_c = 3.11$ $P = 0.083$	$F = 1.51$ $F_c = 2.60$ $P = 0.223$
3	n/a	n/a	$F = 1.19$ $F_c = 3.44$ $P = 0.433$	$F = 1.07$ $F_c = 2.45$ $P = 0.422$	**$F = 4.15$** **$F_c = 2.71$** **$P = 0.010$**
4	n/a	n/a	n/a	$F = 1.27$ $F_c = 3.73$ $P = 0.382$	**$F = 4.94$** **$F_c = 3.97$** **$P = 0.030$**
5	n/a	n/a	n/a	n/a	**$F = 3.88$** **$F_c = 3.69$** **$P = 0.044$**
(b) Velocity					
1	$t = 0.08$ $t_c = 1.67$ $P = 0.493$	$t = 0.47$ $t_c = 1.67$ $P = 0.320$	$t = 0.80$ $t_c = 1.68$ $P = 0.214$	$t = 0.89$ $t_c = 1.68$ $P = 0.190$	**$t = 3.19$** **$t_c = 1.68$** **$P = 0.001$**
2	n/a	$t = 0.37$ $t_c = 1.68$ $P = 0.358$	$t = 0.70$ $t_c = 1.69$ $P = 0.245$	$t = 0.79$ $t_c = 1.69$ $P = 0.217$	**$t = 2.78$** **$t_c = 1.70$** **$P = 0.005$**
3	n/a	n/a	$t = 0.71$ $t_c = 1.70$ $P = 0.242$	$t = 1.52$ $t_c = 1.70$ $P = 0.070$	**$t = 2.70$** **$t_c = 1.94$** **$P = 0.018$**
4	n/a	n/a	n/a	**$t = 1.89$** **$t_c = 1.75$** **$P = 0.039$**	$t = 2.93$ **$t_c = 1.89$** **$P = 0.011$**
5	n/a	n/a	n/a	n/a	**$t = 1.90$** **$t_c = 1.89$** **$P = 0.050$**

Note: Entries in bold show statistically significant differences ($P < 0.05$). The subscript "c" refers to the critical values of the *F* and *t* statistics. n/a, not applicable.

age survey points supporting suitable habitat at respective site optimum Q_i) did not rank in a sequence that corresponded to their position on the sediment supply – transport capacity continuum that underpins their geomorphic classification (Fig. 3).

Rate of change in discharge and spawning

The 2000, 2001, and 2002 spawning period hydrographs are shown along with all observations of spawning activity throughout the Allt a' Ghlinne Bhig (Fig. 8). It is clear that fish avoided periods of the highest flow, as apparent from the discharge electivity index constructed from the data (Fig. 9). However, it is also apparent that specific discharges were used at some times but not at others (asterisks in Fig. 8). Integration of utilized and available rates of change of discharge ($dQ \cdot dt^{-1}$) data to calculate values of electivity indicates that fish avoided rapidly varying flow (Fig. 10). Q_i vs $dQ \cdot dt^{-1}$ is plotted for available and utilized flows (Fig. 11); fish spawned at a relatively high Q_i if it was associated with low $dQ \cdot dt^{-1}$, but not vice versa.

Discussion

There is now considerable interest in linking across multiple spatial scales within hydroecology both to improve the scientific understanding of the factors that influence patterns of species distribution and abundance and to provide a more integrated basis for river and catchment management decisions. Numerous authors have, either explicitly or implicitly, suggested that hierarchical controls influence the distribution of suitable habitats for spawning salmonids (e.g., Montgomery et al. 1999; Buffington et al. 2004; Moir et al. 2004). Thus, at the catchment scale, the interaction of slope, discharge, and sediment supply exerts a strong influence on the distribution of reach types; in turn, this influences where suitable sedimentary and hydraulic microhabitat conditions

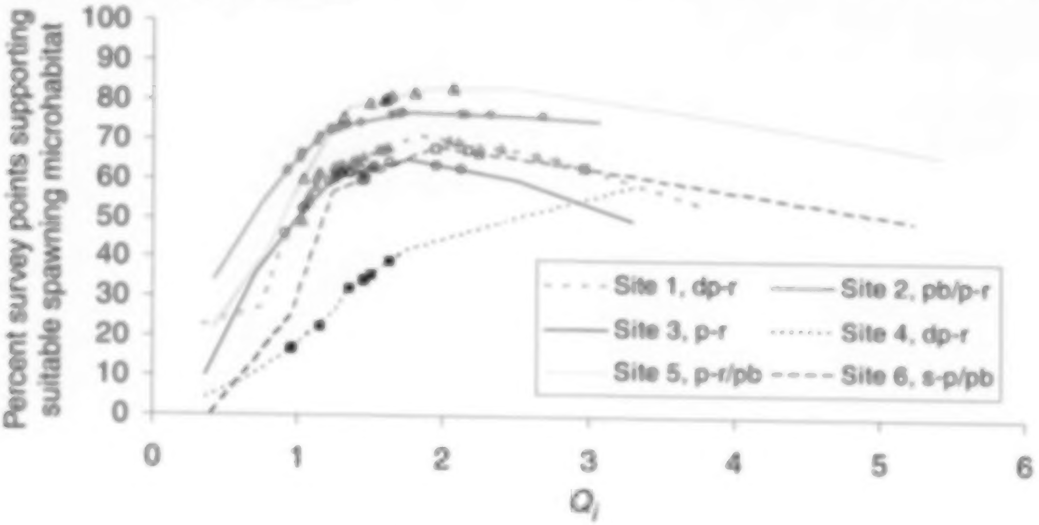


Fig. 7. Relationships between Q_i and the proportion of survey points supporting suitable microhabitat spawning conditions at the six study sites. The length of the lines represents the surveyed flow range at each site. Point markers identify individual spawning observations at each of the study sites (shaded triangles, site 1; shaded circles, site 2; open circles, site 3; solid squares, site 4; open triangles, site 5; open squares, site 6). Reach type classifications (refer to Fig. 3): d p-r, dynamic pool–riffle; p-r, pool–riffle; p-r/pb, transitional pool–riffle/plane bed (pool–riffle dominant); pb/p-r, transitional plane bed/pool–riffle (plane bed dominant); pb, plane bed; s-p/pb, transitional step–pool/plane bed (step–pool dominant).

occur. To understand how changes to flow and sedimentary regimes (through factors such as land-use change or river regulation) within a catchment might affect salmonid populations, it is important to understand the nature of these hierarchical controls. Previous work in the Allt a' Ghlinne Bhig and neighbouring streams assessed how channel morphology and sedimentary conditions influence the catchment-scale distribution of spawning and identified continuous upstream variation in discharge use as a function of channel dimensions (Moir et al. 1998, 2004; Webb et al. 2001). The current work has extended this research by looking more specifically at interactions between channel morphology, discharge, and hydraulics in known spawning areas and how these might affect their suitability and utilization by salmon.

The six study sites enabled characterization of flow–hydraulic relationships across the range of channel morphologies and sizes utilized by fish in the study catchment. This breadth of study would be difficult using 1D or 2D habitat modelling approaches, given their greater data needs. Furthermore, because of problems of accurately simulating hydraulics in steep channels with large roughness elements, it is unlikely that such models would be able to adequately predict hydraulic conditions in the study stream. Unlike other hydraulic rating studies (e.g., Collings et al. 1972; Mosely 1982), the present study explicitly considered the influence of channel morphology on discharge–hydraulic relationships. Also, the resolution of the analysis was improved relative to other studies (e.g., Hogan and Church 1989; Jowett 1998) by the use of percentile values of depth and velocity that permitted assessment of the hydraulic variability across sites at a given discharge. Perhaps the most important difference between the present and other hydraulic rating studies is that an explicit link has been made between hydraulics and stream ecology, in this instance through empirical observations of spawning activity.

The results indicate that Atlantic salmon utilize a wide range of channel sizes and morphologies even within one, relatively small tributary stream. Spawning was observed to occur in dynamic pool–riffle through to transitional step–pool/plane bed morphologies and in channel sizes ranging from 5.1 to 10.3 m mean bankfull width. Q_i vs depth and velocity relationships differed significantly between the sites (ANCOVA, $P < 0.05$), indicating that fish used sites that exhibit quite different hydraulic behaviour.

The precise nature of a site Q_i vs depth or velocity relationship is controlled by lateral and longitudinal channel geometry and roughness elements (grain and form drag components relating to sedimentary character and bedforms, respectively) both within the site and in the adjacent upstream and downstream reaches (Ferguson 1986). Thus, the different hydraulic responses of sites to changes in discharge reflect differences in channel size and morphology. Intercepts of Q_i vs depth and velocity relationships are strongly influenced by channel dimensions; hence, the site with smallest channel dimensions (site 6) was significantly different from the others with respect to both depth and velocity intercepts. However, the slope of the relationship is less influenced by channel size and more closely related to channel morphology. This is best demonstrated through comparison of the hydraulic responses of sites 5 and 6 to discharge changes. Although similar in size, their contrasting morphologies (transitional pool–riffle/plane bed at site 5; transitional step–pool/plane bed at site 6) result in very different hydraulic responses to changing discharge. Site 5 has a pronounced rectangular cross section and a relatively low bed slope (0.0074), which results in a faster rate of change of

Fig. 8. Hydrographs for (*a*) 2000, (*b*) 2001, and (*c*) 2002 spawning seasons, including spawning incidents (shaded ×). Sections highlighted in bold are periods of observation. Asterisks (*) denote periods where spawning is avoided at flows that are utilized at other times during the observation period. Hydrographs are truncated at 7 × Q_r, the approximate limit of unhindered spawning observation.

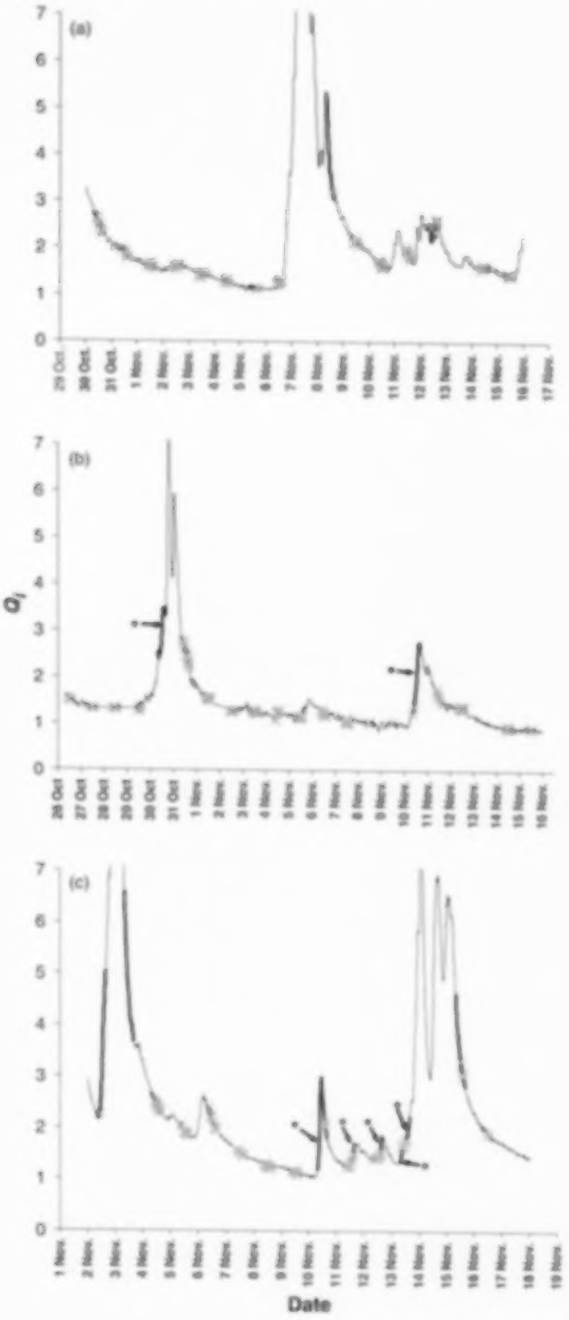


Fig. 9. Relativised electivity index (E^*) distribution for Q_r based on spawning observation and flow data.

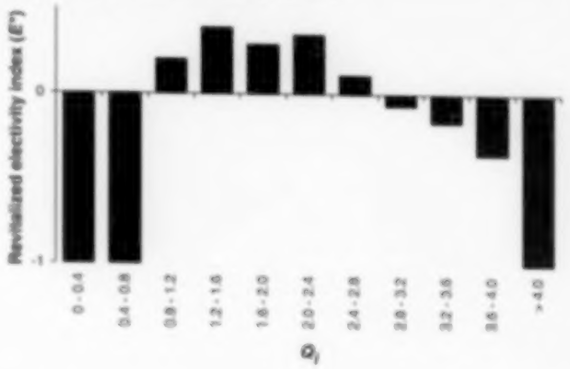
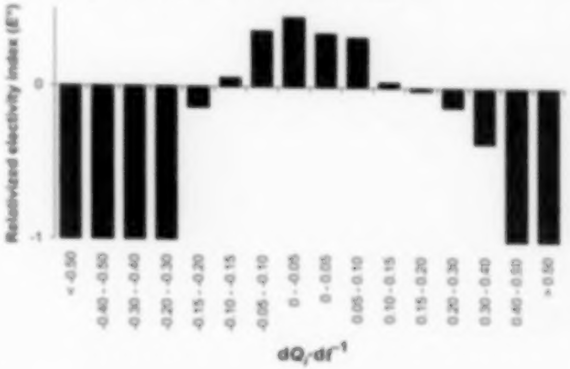


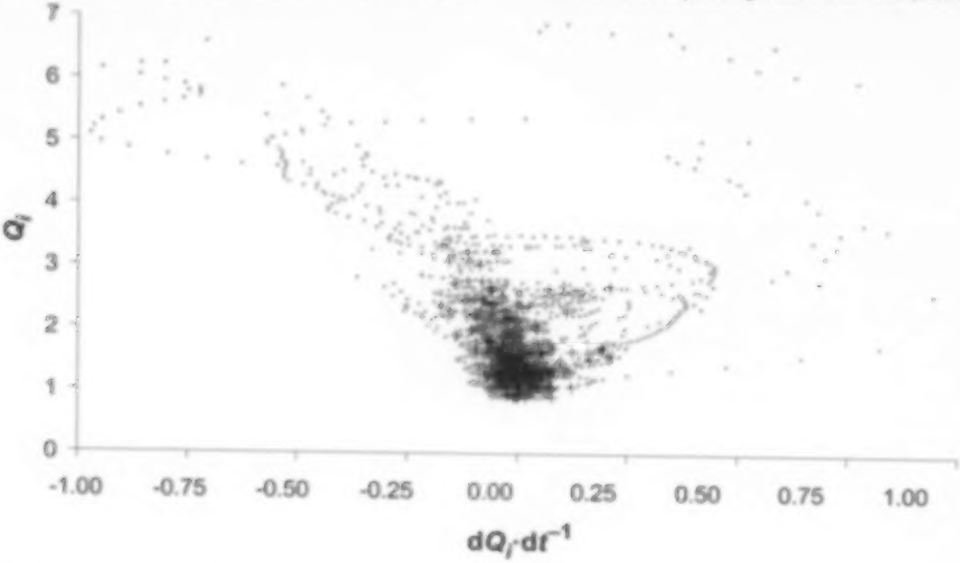
Fig. 10. Relativised electivity index (E^*) distribution for $dQ_r \cdot dt^{-1}$ based on spawning observation and flow data.



depth than velocity with varying flow, i.e., depth exponent > velocity exponent. In contrast, the much steeper slope (0.0446) at site 6 results in flow changes being primarily met through changes in velocity, i.e., velocity exponent > depth exponent. Lee and Ferguson (2002) observed that the accepted general pattern of at-a-station hydraulic geometry exponents being greater for depth than velocity tended to be reversed in steep, step–pool systems. In the Allt a' Ghlinne Bhig, only site 6 exhibited a step–pool dominated morphology and had a velocity exponent that exceeded its depth exponent. The unique morphology and hydraulic functioning of site 6 appears to be reflected in different patterns of relative discharge use compared with the other study sites; the mean and range of Q_r values used at this site were significantly greater than at others. Similar findings were presented by Moir et al. (2004), who showed that spawning in transport reaches (e.g., plane bed and step–pool) occurred under a narrower Q_r range and higher mean Q_r than in response channels (e.g., pool–riffle). In the present study, only site 6 exhibits a transport morphology (step–pool/plane bed).

The general decrease in hydraulic heterogeneity with increasing discharge is a phenomenon widely observed in natural channels and is the result of a reducing influence of bedforms and other roughness elements as they become progressively drowned out (Clifford and Richards 1992;

Fig. 11. Plot of Q_i vs d $Q_i \cdot dt^{-1}$ for flows available to (shaded circles) and utilized by (+) spawning Atlantic salmon (*Salmo salar*).



Stewardson and McMahon 2002). Differences in hydraulic variability between the six study sites are likely to be related to contrasting channel size and morphology. The sites associated with the greatest hydraulic variability (sites 1 and 4, as indexed by the coefficients of variation of depth and velocity) are also those exhibiting the most heterogeneous morphologies. However, the data from the six sites do not support the hypothesis proposed by Moir et al. (2004) that greater hydraulic variability (related to morphological heterogeneity) leads to a greater range of discharges being usable for spawning. For example, site 4 had a reach type classification associated with high morphological heterogeneity (dynamic pool–riffle) and was characterized by high hydraulic variability across the sampled flow range but had the lowest spawning Q_i range. Conversely, site 2 had relatively low hydraulic variability but the highest spawning Q_i range. Similar conclusions can be drawn from the Q_i vs suitable habitat curves in Fig. 7: sites 2 and 5 were predicted as having the highest percent of survey points supporting suitable habitat, but both exhibited relatively homogenous morphologies (plane bed/pool–riffle for site 2, pool–riffle/plane bed for site 5). Conversely, site 4 was characterized as having a highly heterogeneous morphology (dynamic pool–riffle) and was predicted as having a consistently low percent of suitable habitat across the range of surveyed flows. Thus, there were no apparent relationships between the site suitable habitat curves and respective channel morphologies.

Only the area of suitable sediment correlated significantly with the number of fish using individual sites. Thus, overall, there was little evidence of strong hydraulic microhabitat controls on spawning. There were spatial patterns in the relative discharges used in the Allt a' Ghlinne Bhig, with higher minimum Q_i values utilized in the upper catchment compared with the lower catchment. However, depth values at the lower Q_i utilization limit varied little between the sites, suggesting that a hydraulic mechanism controlled this along-stream pattern. Increasing minimum discharge utilization by spawning fish with distance upstream in upland Scottish streams was observed by Webb et al. (2001) and Moir et al. (2004) and was suggested to relate to the minimum depth requirements for access to and (or) utilization of habitats being met at progressively higher relative flows as channel dimensions decreased with distance upstream. Similar findings and explanations have been given by Baxter (1961), Fukushima (1994), and Vadas (2000) for other river systems. During the 3 years of study at the Allt a' Ghlinne Bhig, extreme low flows did not occur and spawning was apparently not impeded by low depths in the larger dimension channel areas (i.e., sites 1–4) where the lowest flows available (~1 × Q_i) were still utilized by spawning fish.

Although consistent hydraulic mechanisms explaining differences in Q_i use between the study sites were not identified, they may exist. The resolution of data obtained with the approach adopted here may be too insensitive to detect other local hydraulic conditions with potential importance for site selection by spawning salmonids (e.g., shear stress, convective acceleration). Also, it is important to recognize that there are factors other than hydraulic characteristics that may influence the suitability of a given reach for spawning. For example, reach type has been shown to be related to grain size characteristics and, therefore, to the availability of suitable salmonid spawning habitat (Montgomery et al. 1999; Buffington et al. 2004). The results of the present study in relating the area of suitable sediment to frequency of spawning demonstrate that substrate may play a dominant role in governing site selection in certain situations. However, site-specific conditions related to the local energy environment and sediment supply can result in heterogeneous morphologies (and therefore high hydraulic complexity) with low quantities of spawning-caliber sediment and, conversely, homogenous morphologies (and low hydraulic complexity) associated with high quantities of suitable sediment. In the present study, site 4 provides an example of the first case (dynamic pool–riffle channel, high morphological and hydraulic complexity, but relatively low percentage (77%) area of suitable sediment), and site 5 is an example of the second case (pool–riffle/plane bed channel, low morphological and hydraulic complexity, but a relatively high percentage area (95%) of suitable sediment). The occurrence and magnitude of hyporheic flow is also related to reach type. For example, the topographic heterogeneity inherent in pool–riffle channels encourages hyporheic flow, producing areas of upwelling and downwelling in relation to variations in hydraulic head. Many studies have linked patterns of surface–hyporheic water exchange to site utilization by salmonids (e.g., Witzel and MacCrimmon 1983; Vronskii and Leman 1991; Curry and Noakes 1995), although there is no consistent agreement as to whether upwelling or downwelling locations are preferred within or between salmonid species. Moreover, it is difficult to determine whether fish actively select spawning habitat based on the nature of hyporheic flow, as the locations exhibiting particular intergravel flow characteristics also tend to be associated with the morphological units that provide the suitable microhabitat (hydraulic and sedimentary) conditions required by fish.

In the Allt a' Ghlinne Bhig, point-by-point microhabitat habitat suitability determined using HSIs did not predict discharge utilization by fish well. The HSIs predicted relatively high values of suitability at $>3 \times Q_t$, whereas such flows were not observed to be used by spawning fish. Similar findings were reported by Gibbins et al. (2002), who compared weighted useable area (WUA) output from a PHABSIM model with observed patterns of discharge utilization at a spawning site on the nearby Girnock Burn. WUA is an indicator of the area of suitable habitat available to a particular life stage of a species within a given modeled reach. It is calculated by integrating the hydraulic (depth and velocity) and sedimentary characteristics for cells across the reach with the suitability of those values as defined by HSIs. Cell suitability values are summed to give an overall value of habitat suitability for the reach across a range of discharges. Gibbins et al. (2002) found that PHABSIM predicted high values of WUA for flows that were actually avoided by spawning fish. Essentially, PHABSIM and the approach used in the current study predict available habitat in the same manner, by relating instream hydraulic data to HSI information. It therefore appears that this approach fails to account for important processes that govern habitat use by spawning Atlantic salmon at higher flows, at least in certain instances.

The temporal stability of microhabitat conditions at higher discharges is potentially one such process. Although discharge certainly controls the distribution of available habitat at a specific point in time, the data for the Allt a' Ghlinne Bhig suggest that the rate of change in discharge may also be important. The apparent avoidance of higher discharges is at least partly due to the autocorrelation of Q_t with $dQ \cdot dt^{-1}$, i.e., higher discharges tend to be associated with periods of higher rates of change in flow. The construction of a redd can take >12 h (Webb and Hawkins 1989), over which time flows can change markedly in small upland catchments such as the Allt a' Ghlinne Bhig. Consequently, channel hydraulics in the vicinity of a redd may alter sufficiently to deter spawning. Spawning fish were observed to temporarily abandon an uncompleted redd during periods of rapidly rising flow during the 2000–2002 study seasons. During such circumstances, they did not attempt to relocate to alternative suitable locations, even though they existed in the same geomorphic unit (as shown by the empirical hydraulic data). Rather, all spawning activity ceased and pairs of fish took up position close to the initial redd at a location that provided some protection from the flow (usually close to the channel banks). Spawning resumed at the initial redd once flows returned to a more stable condition. Given the presumed significance of energy invested in constructing a redd, it would be a more efficient strategy for fish to wait until hydraulics at the initial spawning site had returned to a more stable state rather than to restart excavation at a new location during rapidly changing flow. It is proposed that although relatively high flows will provide suitable microhabitats, these conditions tend to be rather transient and do not persist at any specific location long enough to permit successful spawning. Thus, it is important that in streams such as the Allt a' Ghlinne Bhig, assessment of the relationship between discharge and habitat suitability should consider explicitly the temporal stability of habitat conditions, rather than assuming that each discharge has a fixed suitability value. The observed variations in flow utilization between sites may be related to the manner in which channel dimensions and morphology interact with changing discharge to influence the temporal rather than spatial dynamics of microhabitat hydraulics. Channel morphologies that promote more temporally and spatially stable hydraulic conditions with varying flow are likely to provide suitable spawning habitat over a greater flow range and, thus, over a greater proportion of the spawning period.

Data for the Allt a' Ghlinne Bhig, a small upland stream, indicate that spawning occurs in a wide range of channel sizes and morphologies, with the relationships between discharge and instream hydraulic conditions varying among these. However, the evidence does not support the hypothesis proposed by Moir et al. (2004) that the discharge range over which spawning takes place and, hence, the frequency of utilization of spawning sites are primarily controlled through morphological heterogeneity regulating hydraulic variability. The higher frequency of spawning at sites with greater areas of suitable substrate suggests that sedimentary factors (coupled with channel dimensions) may exert a key influence on utilization. Reach types exhibiting a morphology indicating a higher sediment supply to transport capacity ratio (e.g., pool–riffle) tend to have a higher proportion of the gravel-sized material required by spawning salmonids (Montgomery et al. 1999; Buffington et al. 2004; Moir et al. 2004), so the selection of pool riffle reaches observed in many studies can be at least partly explained by substrate characteristics.

The apparent significance of the rate of change of discharge in the spawning behaviour observed in the Allt a' Ghlinne Bhig has important implications for habitat modelling studies and flow management in regulated systems. The rate of change may be a crucial hydrological variable that habitat models, to date, have largely failed to consider when assessing or making recommendations for environmental flows. Although time series analysis is typically used in PHABSIM-type studies to examine the influence of flow variation on the temporal distribution of habitat (Stalnaker et al. 1994; Dunbar et al. 1996), this does not explicitly account for the rate of change of flow. Work in other rivers, particularly larger and less hydrologically dynamic ones, is needed to determine the broader significance of the rate of change of discharge for spawning Atlantic salmon.

Direct observations of discharge use seem to suggest lower optimum discharges for spawning than methods that combine point hydraulic and sedimentary data with HSIs to predict suitability or habitat area (Gibbins et al. (2002, PHABSIM) and present study). This may be a stream-size or stream-type effect, as the streams in both studies were small, relatively steep upland streams. Correspondence between direct observations and modelled results may improve in other stream sizes or types. Nonetheless, the present study suggests that the assessment of the discharge needs of spawning Atlantic salmon should not be based solely on one approach.

The apparent absence of clear hydraulic preferences of fish spawning in the Allt a' Ghlinne Bhig may reflect that conditions in this relatively undisturbed upland stream were all broadly within the range useable by fish. Comparison of the current results with data from sites less frequently used for spawning, or not used at all, may further improve our understanding of the implication of discharge – channel morphology – hydraulic interactions for fish. Because the selection of specific spawning locations is ultimately dictated by the availability of suitable microhabitat conditions, it is anticipated that the approach of this study in examining the meso-scale (10^1–10^2 m) provision of these conditions across a range of discharges and in contrasting reach types will be useful in understanding the spatial and temporal distribution of spawning activity. Moir et al. (2002) and Crisp and Carling (1989) have demonstrated that selection of microhabitat conditions for spawning forms a continuum within and between salmonid species, with bigger individuals and species tending to use deeper water, higher velocities, and coarser sediment. Therefore, although the specific results of the current work are species- and size-specific, the broad insights gained of the interactions between channel type, discharge, substrate character, hydraulics, and habitat use should apply to other salmonid species.

Acknowledgements

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Decadal changes in the North Sea food web between 1981 and 1991 — implications for fish stock assessment

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Abstract: The North Sea ecosystem of the early 1980s differed substantially from that of the early 1990s. The current North Sea multispecies fisheries assessment models are parameterized by fish diet data sets that reflect both ecosystem states, as the stomachs were sampled in 1981 and 1991. In this study, multispecies virtual population analysis (MSVPA) was parameterized with either diet data set, leading to different model food webs, each representing the predator's diet selection behavior and spatiotemporal overlap with their prey in the two respective ecosystem states. The impact of these changes in predator preferences and spatiotemporal overlap on recruitment success and on stock developments could be demonstrated by using either stomach data set to estimate historic and future spawning stock biomass and recruitment trajectories. The observed changes in the food web mainly impacted the hindcasted recruitment trajectories, whereas spawning stock biomass estimates were quite robust. In the prediction runs, the differences in the survival rate of the recruits decided whether fish stocks of commercially important species (e.g., *Gadus morhua*, *Merlangius merlangus*) would recover or collapse in the near future.

Résumé : L'écosystème de la mer du Nord du début des années 1980 différait considérablement de celui du début des années 1990. Nous avons déterminé les paramètres de modèles courants d'évaluation des pêches multispécifiques de la mer du Nord à partir d'ensembles de données sur le régime alimentaire des poissons qui représentent les deux états de l'écosystème, les estomacs ayant été prélevés en 1981 et 1991. Nous avons donc, dans notre analyse des populations virtuelles multi-spécifiques (MSVPA), introduit les paramètres provenant de chacune des deux banques de données. Nous avons obtenu deux réseaux alimentaires différents, chacun représentant le comportement de sélection alimentaire des prédateurs et le chevauchement spatio-temporel de leurs proies dans les deux états respectifs de l'écosystème. Nous avons pu démontrer l'impact de ces changements dans les préférences des prédateurs et dans le chevauchement spatio-temporel sur le succès du recrutement et le développement des stocks en utilisant l'une ou l'autre des banques de données de contenus stomacaux pour estimer la biomasse des stocks reproducteurs passés et futurs ainsi que les trajectoires du recrutement. Les changements observés dans le réseau alimentaire affectent surtout les trajectoires de recrutement reconstituées, alors que les estimations de biomasse des stocks sont très robustes. Dans les essais de prédiction, les différences de taux de survie des recrues permettent de décider si les stocks de poissons d'espèces d'importance commerciale (par ex., *Gadus morhua*, *Merlangius merlangus*) vont se rétablir ou s'effondrer dans un avenir rapproché.

[Traduit par la Rédaction]

Introduction

During the last two decades, all trophic levels of the North Sea ecosystem have undergone substantial climatically induced changes (e.g., Beare et al. 2004; Beaugrand 2004) culminating in a potential regime shift around 1987 (e.g., Reid et al. 2001*a*, 2001*b*; Beaugrand 2004). Superimposed on climate forcing, the commercial fisheries also altered the structure and functioning of the fish assemblage (Heath 2005).

Multispecies virtual population analysis (MSVPA; Helgason and Gislason 1979; Pope 1979) was developed as an extension of the single-species VPA (SSVPA; Gulland 1965) to be able to take changes in food webs into account in fisheries management advice. Analyses using the MSVPA methodology have shown that predation on young fish is especially variable over time and should be taken into account when trying to produce more reliable mid- to long-term predictions (Magnusson 1995). Traditional single-species assessment techniques ignore this information (Magnusson 1995; ICES 2005*a*), although predator (e.g., Atlantic cod, *Gadus morhua*) recovery scenarios, which are at the agenda of current management efforts by the European

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Commission (e.g., European Commission 2002), show marked deviations in prediction results depending on which assessment method is used (ICES 2003).

The central elements for the calculation of predation mortalities inside MSVPA are suitability coefficients, also simply called suitabilities. These coefficients are implicit measures of what a predator "likes to eat" in terms of prey species and prey size preferences, but they also implicitly reflect the availability of a certain prey to a certain predator as a result of predator–prey overlap in space and time (Sparre 1991). Mathematically, suitability coefficients (*S*) are derived by contrasting the relative weight share (*U*) of a prey in sampled stomachs of a predator with the quarterly mean available stock biomass of this prey in the sea ($\bar{N}$·WP, where WP represents mean weight of a certain prey in the stomachs of a certain predator; eq.1). This calculation has to be made for every single interaction (prey species *s* of age *a* is eaten by predator species *p* of age *j* in quarter *q* and year *y*). To standardise the values for the suitability coefficients between 0 and 1 and to allow for statements on the relative suitability of each prey type in contrast to all others, the suitability coefficients have to be divided through the sum over all suitability coefficients relevant for a certain predator (N_S, number of prey species; N_A, number of prey age groups). Thus, if the biomass of all prey types in the sea is known, the suitability coefficients can be calculated, because the relative stomach contents are derived directly from sampled stomach data. There are no extra coefficients for predator–prey overlap or size preferences, for example. These measures are implicitly deduced by contrasting the stomach contents with what is in the field for every single predator–prey interaction (~3000 in the North Sea MSVPA). The biomasses for the different prey types, however, are calculated inside the model with the help of further input data such as catch-at-age data or consumption rates and iterative calculation techniques. Iterative approximation methods are needed, because for the calculation of prey biomasses, predation mortalities and suitability coefficients must be known, although these depend again on prey biomass.

Once suitability coefficients have been calculated for all predator–prey interactions in the MSVPA (suitability matrix), relative stomach contents are predicted for years without stomach data available (eq. 2; for a detailed describtion of MSVPA theory see Sparre (1991) or Magnusson (1995)), as suitability coefficients are treated as being time-invariant.

$$(1)\qquad S_{y,q,p,j,s,a}=\frac{\dfrac{U_{s,a,y,q,p,j}}{\bar{N}_{s,a,y,q}\cdot \mathrm{WP}_{s,a,y,q,p,j}}}{\displaystyle\sum_{s=1}^{N_S}\sum_{a=0}^{N_A(s)}\frac{U_{s,a,y,q,p,j}}{\bar{N}_{s,a,y,q}\cdot \mathrm{WP}_{s,a,y,q,p,j}}}$$

$$(2)\quad U_{s,a,y,q,p,j}=\frac{\bar{N}_{s,a,y,q}\cdot \mathrm{WP}_{s,a,y,q,p,j}\cdot S_{s,a,y,q,p,j}}{\displaystyle\sum_{s=1}^{N_S}\sum_{a=1}^{N_A(s)}\bar{N}_{s,a,y,q}\cdot \mathrm{WP}_{s,a,y,q,p,j}\cdot S_{s,a,y,q,p,j}}$$

To make MSVPA practicable for fisheries assessment, the model is characterised by simplifications (Sparre 1991). Because of the lack of sufficient data, only the most important commercial prey species (so-called MSVPA prey species) are fully parameterized in the model. All other prey species found in the stomach samples (e.g., copepods, euphausiids, nonassessed fish species) are aggregated into one big category called "other food". This category is assumed to have a constant biomass of 30 million tonnes (t) per year. Otherwise, "other food" is treated as an additional prey species. Because the relative weight shares of "other food" are known directly from the stomach samples, the calculations of suitability coefficients and predation mortalities are identical to those of the other MSVPA prey species. The pooling of all prey species, besides the commercially important ones, ignores the fact that predator preferences are not equal for all prey species inside "other food". The assumption of a time-invariant biomass does not take into account any population fluctuations of "other food" species. This could in turn lead to an over- or under-estimation of predation mortalities for the MSVPA prey species.

As further simplification, suitability coefficients are assumed to be constant over time. Suitability coefficients derived from model hindcasts are used to calculate future predation mortalities. If stomach data from more than one year are available, average suitability coefficients are calculated. The assumption of constant suitabilities in the diet selection model translates into a Holling type II functional feeding response (Holling 1959; Magnusson 1995) with no dependence of predator preferences on prey abundances. However, a Holling type III relationship including positive or negative prey-switching behaviour of predators is discussed as a more realistic functional feeding response type (e.g., Rice et al. 1991; Rindorf et al. 1998). The implementation of one or the other functional feeding response could significantly change the calculated predation mortalities, especially for stocks at low abundance levels (Magnusson 1995; Floeter et al. 2005). With MSVPA being a single area model for the entire North Sea, constant suitabilities also imply a time-invariant predator–prey overlap (Magnusson 1995; Hilden 1988). For example, changes in the spatial distribution of predator and prey stocks resulting from climate forcing or density-dependent changes in the realized habitat (e.g., Blanchard et al. 2005) are thus assumed to be negligible for the use of MSVPA in fisheries management. A further important consequence of constant suitabilities is that stomach content data from one year are sufficient to parameterize the entire time series of the MSVPA model. If the assumption of constant suitabilities is correct, the use of stomach data from any other year should not change the suitability coefficients and thus also should not change the calculated predation mortalities. This would reduce the management costs of parameterizing the data, demanding MSVPA to a more tolerable level.

The assumption that the total quarterly consumption per predator can be held constant during the entire calculation time period is the third major model simplification. Therefore, predators can not starve in the model. It is assumed that predators shift their diet towards "other food" when the assessed prey species (e.g., sandeel, herring, Norway pout, 0-group gadoids) become rare in the field.

For the North Sea, only two complete stomach data sets that cover the entire area over four quarters of the year exist to calculate two independent suitability matrices for comparative suitability analyses. These two data sets from the so-called "years of the stomach" in 1981 and 1991 (Daan 1989;

Hislop et al. 1997) were used by the Multispecies Assessment Working Group (MAWG) to test the assumption of time-invariant suitability coefficients (ICES 1992*a*, 1995, 1997). Although for some predators marked deviations from the 1:1 line occurred in plots where suitabilites from 1981 were contrasted with the respective suitabilities derived from the 1991 stomach data set (ICES 1995), the MAWG stated "similarities are greater than the differences" (ICES 1997). However, the observed suitability changes were not analysed in detail for predator–prey interactions separately, and also the question of whether observed suitability changes between 1981 and 1991 were random or systematic could not be answered by the MAWG.

The starting point for the work presented here was to analyse the suitability changes between 1981 and 1991 and, in addition, the role of "other food" in the diet of predators in a more detailed way. For this purpose, MSVPA hindcast and multispecies forecast (MSFOR) runs were carried out with the multispecies assessment tool 4M (Vinther et al. 2002), which is the standard multispecies model suite used in the International Council for the Exploration of the Sea (ICES) community. Furthermore, the uncertainties in current multispecies fisheries assessment due to ignoring potential changes in suitability coefficients and in the amount of "other food" consumed were evaluated. Historic time series of spawning stock biomasses (SSBs) and recruitment biomasses were reconstructed by using either the 1981 or the 1991 model input stomach data set. Also, prediction scenarios were calculated to assess the influence of the historically observed changes in the North Sea food web between 1981 and 1991 on future recruitment success and stock developments.

Material and methods

Data

The stomach data used to parameterize the 4M model stem from the years 1981 and 1991 (Daan 1989; Hislop et al. 1997). Under the auspices of ICES, within every four quarters of 1981 and 1991, a large number of fish predator stomachs were collected in the entire North Sea area (ICES roundfish areas 1–7) to provide input data for MSVPA (Table 1). Detailed descriptions of sampling and stomach content analysis procedures are provided by Robb (1991).

If not stated otherwise, all other model input data were the same as those used in the MSVPA key run 2003 conducted by the Study Group on MultiSpecies Assessment in the North Sea (ICES 2003). These are, namely, data for catch-at-age, consumption rates, proportion mature, mean weight-at-age, and residual mortality.

MSVPA model runs

Two MSVPA model runs were carried out with 4M. Both model runs differed in the use of the stomach data set, otherwise they were completely identical (e.g., the same catch-at-age data and consumption rates were used). One model run was parameterized with the 1981 stomach data only (run 81); for the other run (run 91), only the 1991 stomach data were used. Atlantic cod, whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarkii*), sandeel (*Ammodytes* spp.), and saithe (*Pollachius virens*) were included in the calculations (Table 2). Predators for which stomach data were only available for one of the two stomach data years (e.g., *Eutriglia gurnardus*, *Raja* spp.) were excluded to enable consistent comparative analyses between runs 81 and 91.

Table 1. Numbers of stomachs sampled in 1981 and 1991 (Daan 1989; Hislop et al. 1997).

	Stomach data year	
Predator species	1981	1991
Atlantic cod (*Gadus morhua*)	11 333	9 706
Whiting (*Merlangius merlangus*)	18 908	38 404
Haddock (*Melanogrammus aeglefinus*)	17 241	12 893
Saithe (*Pollachius virens*)	3 420	3 219

To stabilize the results for the terminal years, a multispecies VPA tuning was carried out for each run by applying the method described in Vinther (2001). Tuning fleets and options were used as in the single-species assessments for ICES area IV (e.g., ICES 1999, 2000).

Changes in suitability coefficients

Suitability coefficients derived from runs 81 and 91 were extracted from the output tables of 4M and manipulated in further steps: if a predator–prey interaction did exist in only one of the two runs, the missing suitability coefficient was assumed to be zero in the other run. As in the model, suitability coefficients above a certain species-specific age threshold are set as constant for older predator age groups; interactions with age groups higher than these thresholds were omitted.

Differences in suitability coefficients derived from the 1981 and 1991 stomach data sets were analysed for every age-specific predator–prey interaction by subtracting the 1991 values from the respective 1981 values. Box-and-whisker plots (using SPSS®; SPSS Inc., Chicago, Illinois) were constructed to visualize the distributions and magnitudes of suitability changes. Second, bar charts showing the changes in more detail were plotted for all predators exemplarily for one quarter. For this purpose, the suitability differences were summed for every prey species (eliminating the dimension of prey age) to make shifts in predator preferences and prey availabilities more visible. The presentation of all predator and quarter combinations was not possible because of the number of combinations ($n = 16$). However, examples that are representative of all other combinations were chosen.

Analysis of changes in the share of "other food" in the diet

The observed North Sea wide mean relative stomach contents of predator p, age group j, for prey s, age group a, in quarter q and year $y = 1991$ were predicted with the MSVPA diet selection model and the assumption of constant suitability coefficients (eq. 3). The suitability coefficients for every predator–prey interaction were extracted from run 81 (Suit81), as well as the mean weight of a certain prey in the stomachs of a certain predator (WP81). Both variables were

Table 2. Classification of included species as predator and prey.

Only predator	Predator and prey	Only prey
Saithe (*Pollachius virens*)	Atlantic cod (*Gadus morhua*) Whiting (*Merlangius merlangus*) Haddock (*Melanogrammus aeglefinus*)	Atlantic herring (*Clupea* harengus) European sprat (*Sprattus sprattus*) Norway pout (*Trisopterus esmarkii*) Sandeel (*Ammodytes* spp.)

applied to the prey field of 1991 (mean prey abundances = $\bar{N}91$, N_S is the number of prey species, and $N_A(s)$ is the maximum age group of a certain prey species) calculated with run 91 (eq. 3). The predicted 1991 relative stomach contents (*U*91_predicted) of "other food" were contrasted with the relative stomach contents observed in the 1991 stomach data set. If suitabilities are constant and the treatment of "other food" inside MSVPA is correct, observed and predicted relative stomach contents of "other food" are expected to be almost equal and to show only limited randomly distributed differences. The deviances between model predictions and stomach samples were analysed for every predator species and predator age group in the four quarters of the year 1991:

$$(3) \qquad U91\_\text{predicted}_{s,a,91,q,p,j} = \frac{\bar{N}91_{s,a,91,q}\cdot \text{WP81}_{s,a,81,q,p,j}\cdot \text{Suit81}_{s,a,81,q,p,j}}{\sum_{s=1}^{N_S}\sum_{a=1}^{N_A(s)}\bar{N}91_{s,a,91,q}\cdot \text{WP81}_{s,a,81,q,p,j}\cdot \text{Suit81}_{s,a,81,q,p,j}}$$

Differences in model hindcasts

From runs 81 and 91, the spawning stock biomasses (number of individuals × the proportion mature in each age group) in the first quarter of each hindcast year (1963–2001) were extracted for all species. This was also done for the calculated historic annual mean fishing mortality coefficients (*F*) acting on the age groups higher than zero of each stock. *F* is derived by dividing the numbers caught per quarter from a certain species and age group by the quarterly mean stock numbers in the field.

Because predation mortalities are most important for 0-group fish (e.g., Daan 1973, 1975; ICES 2005*a*), the age-0 recruitment numbers of the third quarter of each year were analysed, as well as the calculated historic predation mortality coefficient (*M*2) trajectories for these recruits. The *M*2 values constitute the ratio between numbers eaten per quarter and quarterly mean stock numbers in the sea.

The historic time series of SSB and recruitment biomass, as well as fishing and predation mortalities, from runs 81 and 91 were compared for all MSVPA species.

Differences in forecasted stock development

To assess the importance of the changes in the North Sea food web for future stock trajectories, midterm prediction scenarios from 2002 to 2010 were carried out with MSFOR using different combinations of input data (stock–recruitment relationships (SRRs), suitability matrix, fishing mortalities) from runs 81 and 91 (Table 3). For example, stock–recruitment curves fitted with the results of the run 81 hindcast were combined with the run 91 suitability matrix to conduct the predictions (run 8191). By mixing these input data, changes in the food web between hindcast and prediction time period in the same order of magnitude as observed in the field between 1981 and 1991 were simulated.

Table 3. Parameterisation of model prediction runs: combinations of input data from the hindcast multispecies virtual population analysis (MSVPA) runs.

Stock–recruitment relationship, initial stock numbers, and future fishing mortalities	Suitability matrix	Prediction run
Run 81	Run 81	Run 81
Run 81	Run 91	Run 8191
Run 91	Run 81	Run 9181
Run 91	Run 91	Run 91

For all scenarios, the future third-quarter age-0 recruitment estimates were calculated by fitting a Ricker stock–recruitment curve (Ricker 1954) to the calculated SSBs and recruitment numbers from the respective MSVPA runs with a subroutine of the 4M package using the Levenberg Marquardt algorithm (Vinther et al. 2002). A constant future fishing mortality matrix was applied consisting of mean species- and age-specific fishing mortalities calculated from 1999 to 2001 in the respective hindcasts. SSB trajectories for all prediction scenarios were compared.

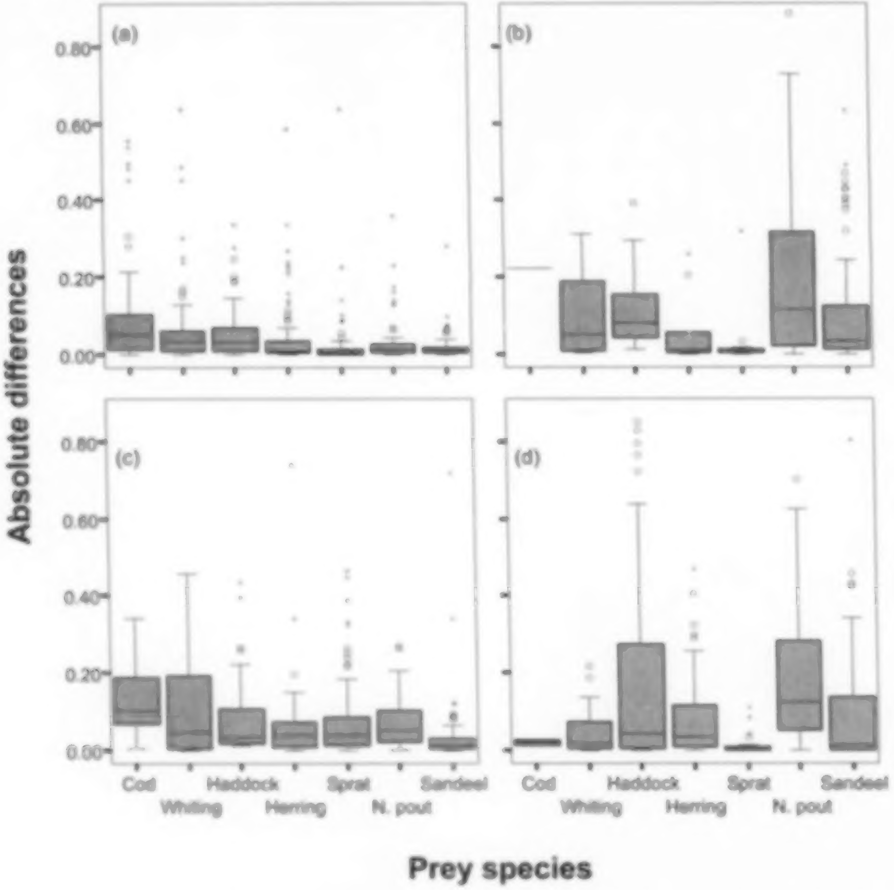
Results

Changes in suitabilities

The two model runs, 81 and 91, revealed some differences in suitability coefficients for a number of predator–prey interactions (Fig. 1). However, most 75th percentiles for observed absolute changes in suitability coefficients were below a difference of 0.2, the median was mainly around 0.1. For all predators, outliers and extreme values existed. The maximum values of absolute suitability changes were in the range of 0.6 to 0.8, which included important predator–prey interactions such as cod–whiting, whiting–herring, and saithe–sandeel.

When looking exemplarily into details of predator–prey interactions, systematic changes in suitabilities became obvious (Fig. 2). In such cases, all predator age groups showed suitability changes in the same direction for a particular prey species. For example, all age groups of whiting had a considerably stronger tendency towards cannibalism in the first quarter of 1991 (run 91) than in the first quarter of 1981 (run 81). As a second example, a strong tendency of changed preferences and (or) availabilities between two prey species could be observed for haddock as a predator in the third quarter. In run 81, Norway pout was clearly the most pre-

Fig. 1. Overview of absolute differences of suitabilities between the stomach data years 1981 and 1991. Each data point reflects changes for a specific predator–prey interaction (predator species *p*, age group *j*, preys on prey species *s*, age group *a*, in a specific quarter. The boxes show the median and 25th and 75th percentiles. Whiskers show the range of absolute differences, which are less than 1.5 times the interquartile distance (height of the boxes) away from the upper or lower margin of the boxes. Outliers (1.5 to 3 times the interquartile distance away from the upper or lower margin of the boxes) are indicated by circles, extreme values (more than 3 times the interquartile distance away from the upper or lower margin of the boxes) are indicated by stars. Box-and-whisker plots are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) whiting (*Merlangius merlangus*), (*c*) haddock (*Melanogrammus aeglefinus*), and (*d*) saithe (*Pollachius virens*). N. Pout, Norway pout.



ferred and available prey species for almost all haddock age groups. In run 91, the situation had changed completely, and sandeel was the most preferred and available prey species.

In some cases, the direction of suitability changes differed between younger and older predator age groups. For example, in the saithe – Norway pout interaction in the first quarter, the predator age groups 3–5 showed higher suitability coefficients in run 91, whereas in age groups 6–9, the reverse was found. Further examples of such systematic suitability changes occurred for all predator species. Cod, however, showed the weakest tendency towards these patterns.

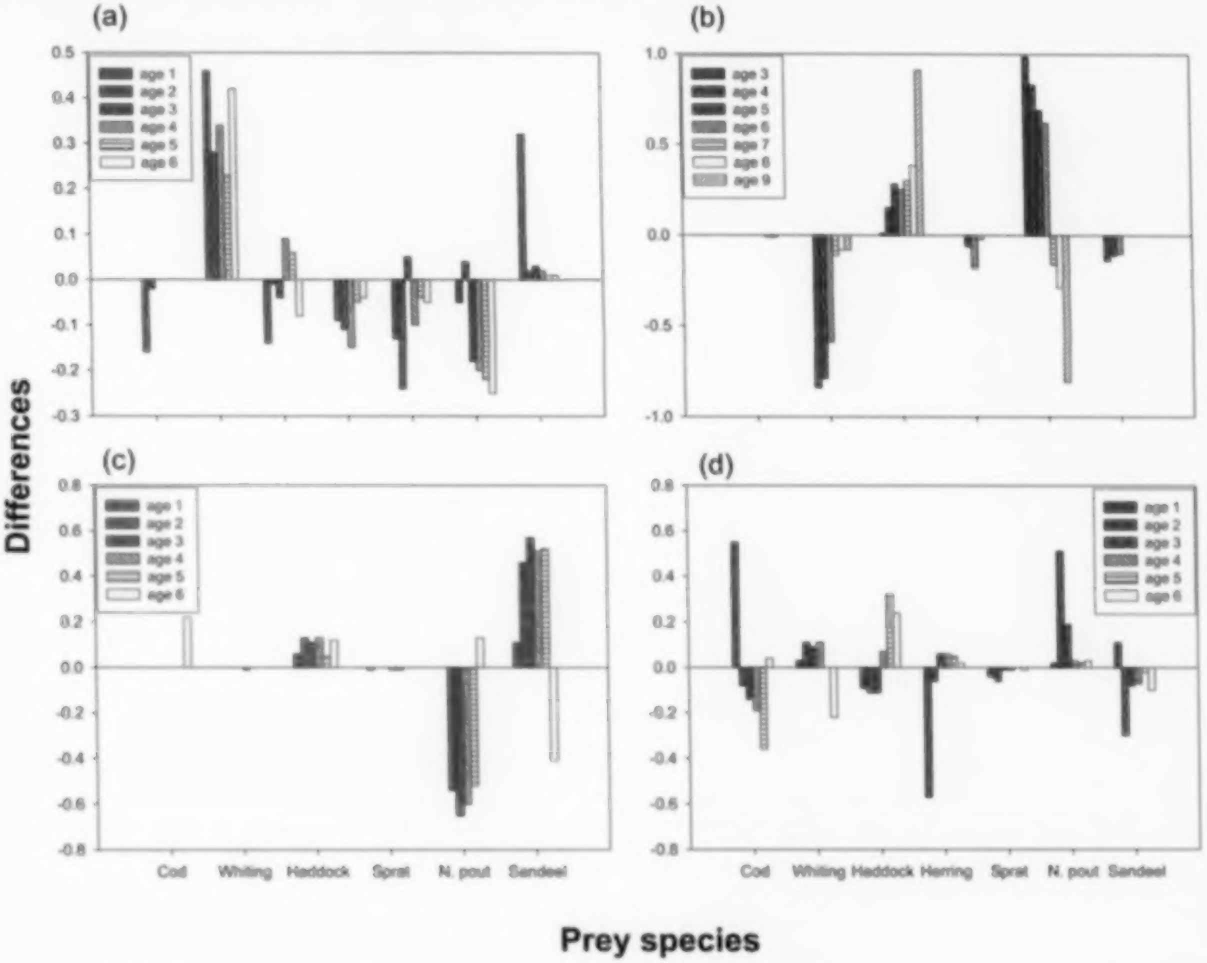
Prediction of the share of "other food" in the stomachs

Generally, the prediction of the share of "other food" in the stomachs using the current MSVPA diet selection model did not closely match the observed share of "other food" in 1991 (Fig. 3). When contrasting observed and predicted relative shares, over- and under-estimations occurred for all predators. For cod, the tendency to overestimate the share of "other food" increased with increasing predicted values (up to residuals of >0.3, with a value of 1 as theoretical maximum). The same pattern of systematic overestimations could be observed for saithe, but with higher values of the residuals (up to 0.95).

Likewise in whiting, in only five out of 24 cases, representing different quarter and age-group combinations, an underestimation could be observed. In all other cases, overestimations mostly in the range of residual values 0.1 to 0.3 occurred.

A clear separation between the tendency of over- and under-estimations occurred for haddock. Estimated relative shares under 0.5 constituted a clear underestimation in most

Fig. 2. Differences between summed 91 and summed 81 suitabilities for selected prey species by quarter and predator age groups. Positive differences depict higher summed suitabilities in 1991. Negative differences imply that the summed suitabilities of 1981 are higher. "Other food" is not displayed. Differences in suitability coefficients are shown for (*a*) whiting (*Merlangius merlangus*) in the first quarter, (*b*) saithe (*Pollachius virens*) in the first quarter, (*c*) haddock (*Melanogrammus aeglefinus*) in the third quarter, and (*d*) Atlantic cod (*Gadus morhua*) in the second quarter. N. Pout, Norway pout.



cases compared with the observed values (residuals up to –0.9), whereas for estimates above 0.5, this tendency changed to an overestimation (residuals up to 0.48).

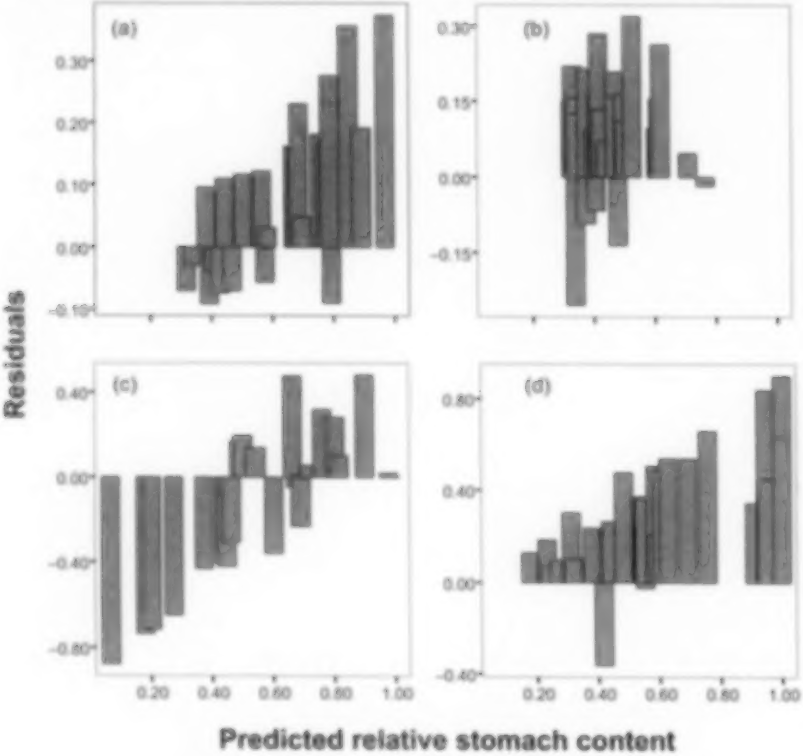
Hindcast

Hindcast results differed between runs 81 and 91, especially for the time series of back-calculated historic recruitment biomasses (Fig. 4). The magnitude of calculated recruits was generally higher in run 91 than in run 81 (e.g., cod recruitment biomass in 1980 = 9 × 10^3 t in run 81 but 141 × 10^3 t in run 91). Only for herring were higher values calculated in run 81. For haddock, no clear tendency could be found. For the most recent years of the investigated time period, the absolute deviations between both runs became smaller for most species. The percentage differences, however, remained at high levels, e.g., in year 1997 cod recruitment biomass was estimated as 0.353 × 10^3 t in run 81 and 2.12 × 10^3 t in run 91. This corresponds to an absolute difference of only 1.77 × 10^3 t, but a relative difference of 501%.

The calculated recruitment biomass trajectories in both runs often followed the same long-term trend over the years; however, exceptions did occur, e.g., sandeel. The recruitment estimates for sandeel were characterized by large interannual fluctuations without a clear long-term trend in run 81. In contrast, a long-term declining trend between 1980 and 1997 can be observed in run 91. As a result, the r^2 value of a regression between run 91 and run 81 recruitment numbers was only 0.32.

Historic predation mortality coefficient trajectories showed the same tendency of being higher in run 91 than in run 81 for most species (Fig. 5). For cod and sandeel, run 91 esti-

Fig. 3. Residuals observed when contrasting predicted relative stomach contents for "other food" in 1991 with relative stomach contents of "other food" observed in 1991. Each bar represents the residuals from the line of equality for a single predator age group in a single quarter. Positive values depict overestimations and vice versa. Maximum residuals are ±1. Bar charts are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) whiting (*Merlangius merlangus*), (*c*) haddock (*Melanogrammus aeglefinus*), and (*d*) saithe (*Pollachius virens*).



mates were up to three times higher. For the other species, the differences were clearly smaller (0% to 50% deviances). The long-term trends in historic predation mortality coefficients were fairly similar in both runs for most species, except for sandeel. Here, a long-term declining trend was calculated in run 91, whereas in run 81, the predation mortality coefficients were on a stable level over the entire calculation time period. The very low *M*2 values for sprat reflect the fact that age-0 groups were rarely found in the predators stomachs in the third quarter. In this quarter, mainly age-1 group sprat were eaten (mean *M*2 over all years for third-quarter age-1 sprat: 0.524 in run 91, 0.057 in run 81).

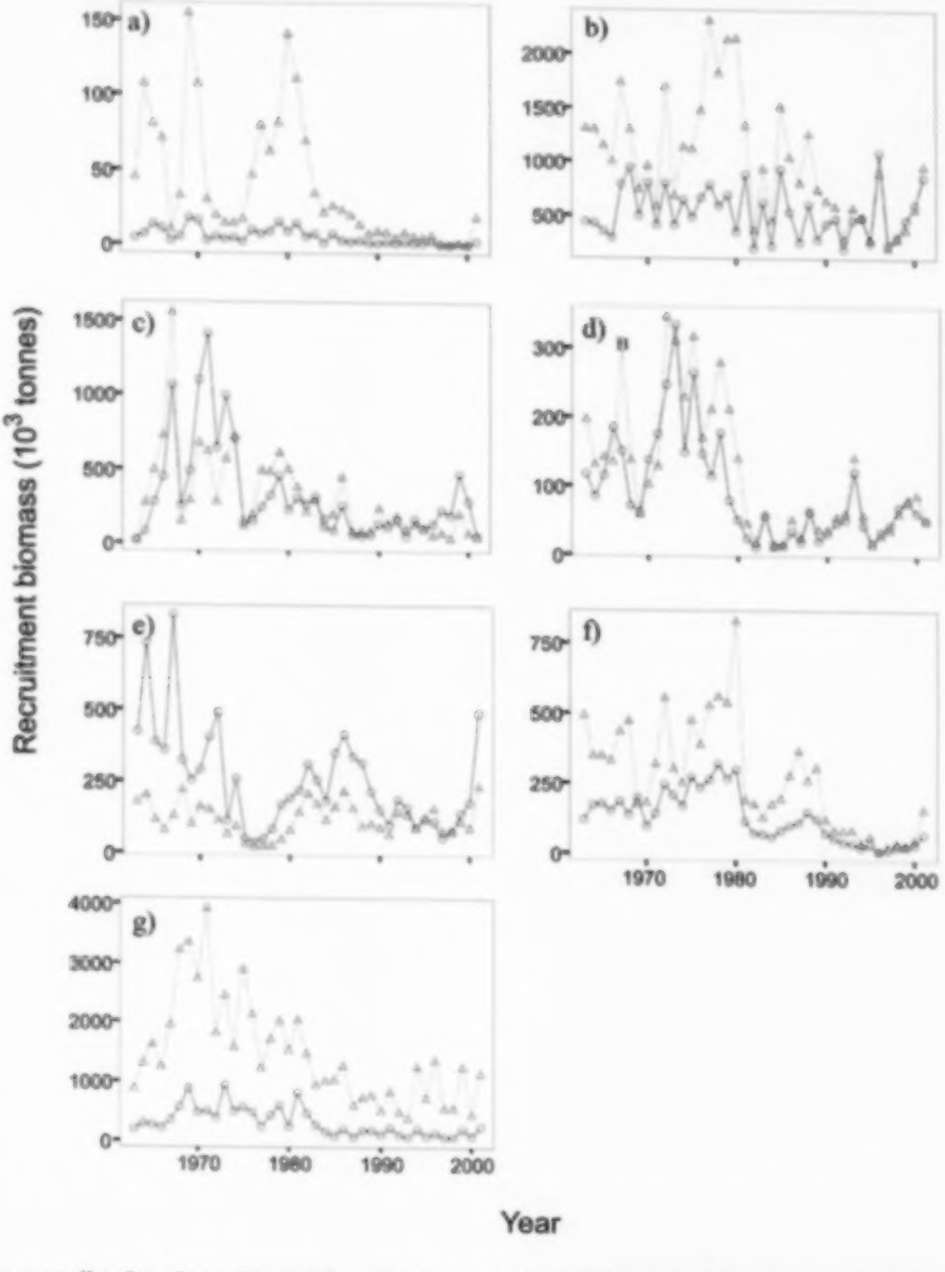
Differences in the calculated historic spawning stock biomasses also occurred, but were smaller than for the recruitment biomasses (Fig. 6). For cod, haddock, and sandeel, the calculated SSBs were nearly identical in both runs. Only for Norway pout were differences in calculated SSBs more pronounced. Between 1988 to 2001, a more or less stable and low SSB (SSB in 2001 = 112×10^3 t) was calculated in run 81. However, in run 91, a strong increasing trend was calculated until 2001 (SSB 2001 = 606×10^3 t). Similar differences in Norway pout SSB trends could be observed for the period between 1963 and 1978. In general, Norway pout SSB trends were quite different over the entire time series (regression between run 81 and run 91 SSB estimates with a r^2 value of 0.24).

The low differences in SSB and the utilization of identical catch-at-age data in both runs led to nearly identical estimated historic fishing mortality coefficients (Fig. 7). Again, only for Norway pout did higher differences in the magnitude of *F* occur. The run 81 estimates were up to two times higher than the run 91 estimates as a result of lower SSB values calculated in run 81.

Stock–recruitment relationships

The SRRs fitted to the results from the respective hindcasts differed in their parameter values between runs 81 and 91 (Table 4). Differences occurred especially for α, the so-called reproductivity parameter (the number of recruits per unit SSB at low stock size). Higher values for α indicate higher recruitment numbers at low stock sizes and vice versa. Differences in α translate directly into differences in the recruitment numbers entering the stocks in the respective forecasts. For cod, in run 81, an α value of 8.43 was calculated, whereas in run 91, α = 64.35; therefore at low stock levels, the SRR of run 91 provided much higher recruitment numbers for the same SSB than run 81. The same statement can be made for whiting, Norway pout, sandeel, sprat, and haddock. However, for these species, the proportional differ-

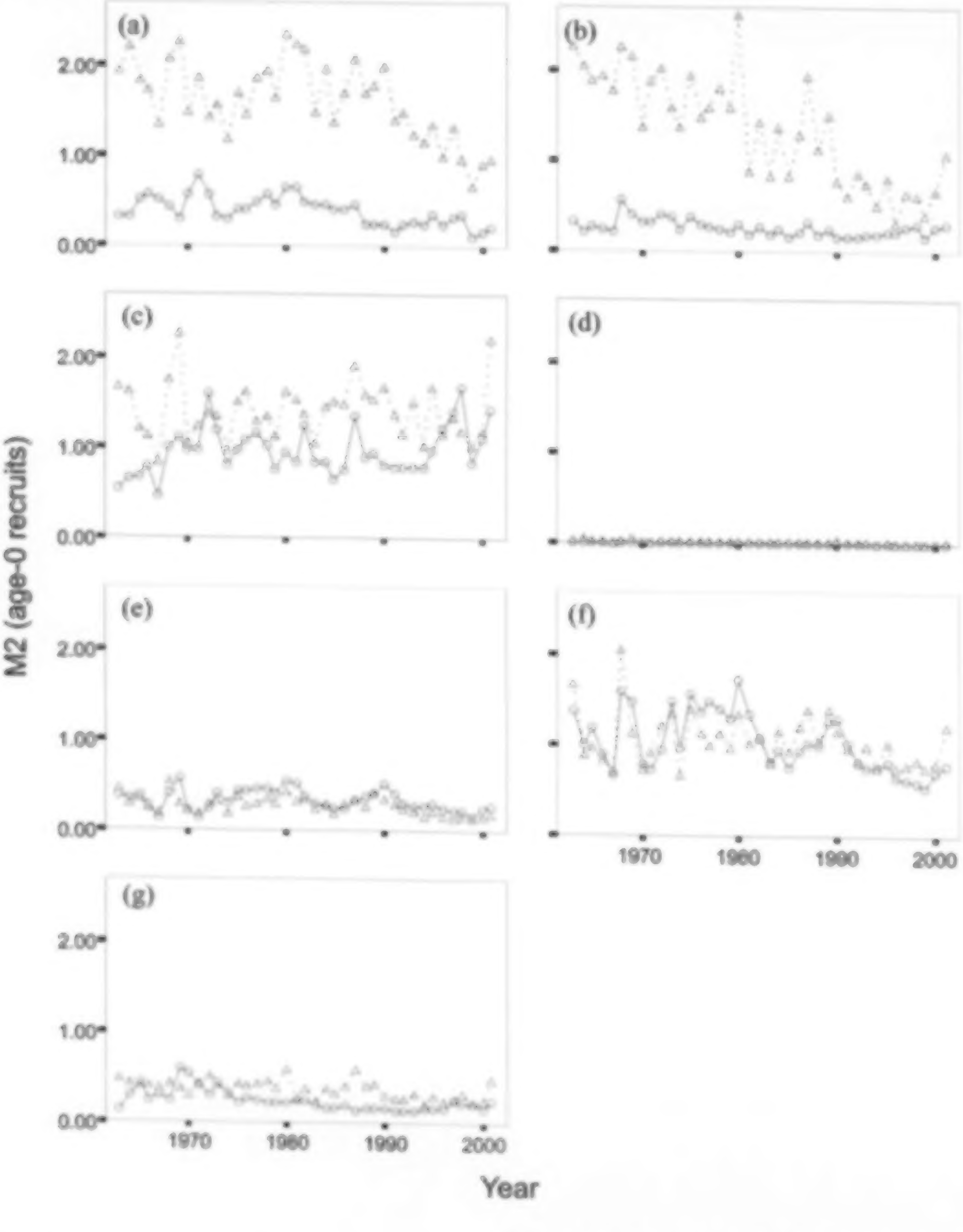
Fig. 4. Comparison of multispecies virtual population analysis hindcast results between run 81 and run 91 according to recruitment biomasses (third-quarter age-0 recruits): run 81, line with circles; run 91, broken line with triangles. Graphs are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) sandeel (*Ammodytes* spp.), (*c*) haddock (*Melanogrammus aeglefinus*), (*d*) European sprat (*Sprattus sprattus*), (*e*) Atlantic herring (*Clupea harengus*), (*f*) whiting (*Merlangius merlangus*), and (*g*) Norway pout (*Trisopterus esmarkii*). Saithe (*Pollachius virens*) as predator only is not displayed.



ences in α were smaller than those observed for cod. Herring was the only species for which the run 81 SRR gave higher recruitment estimates than the run 91 SRR.

The scaling parameter β determining the carrying capacity of an ecosystem for a certain species also differed between both runs. Except for Norway pout, all species had a higher β value in run 91. Higher β values imply that the turning point at high SSBs, where density-dependent factors start to reduce absolute recruitment numbers in the Ricker recruitment curves, is reached at lower SSB values.

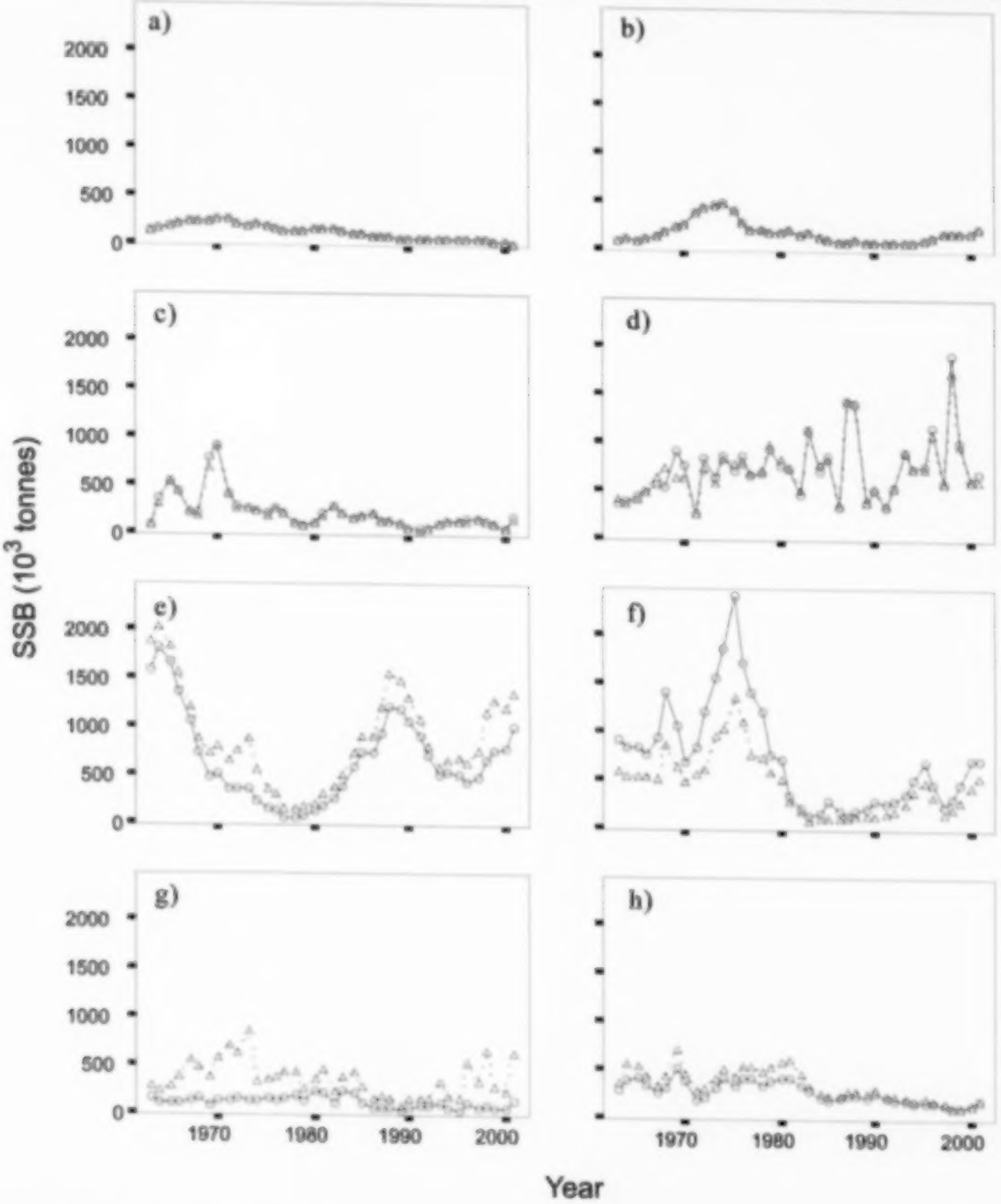
Fig. 5. Comparison of multispecies virtual population analysis hindcast results between run 81 and run 91 according to predation mortality coefficients (*M2*): run 81, line with circles; run 91, broken line with triangles. Graphs are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) sandeel (*Ammodytes* spp.), (*c*) haddock (*Melanogrammus aeglefinus*), (*d*) European sprat (*Sprattus sprattus*), (*e*) Atlantic herring (*Clupea harengus*), (*f*) whiting (*Merlangius merlangus*), and (*g*) Norway pout (*Trisopterus esmarkii*). Saithe (*Pollachius virens*) as predator only is not displayed.



Forecast

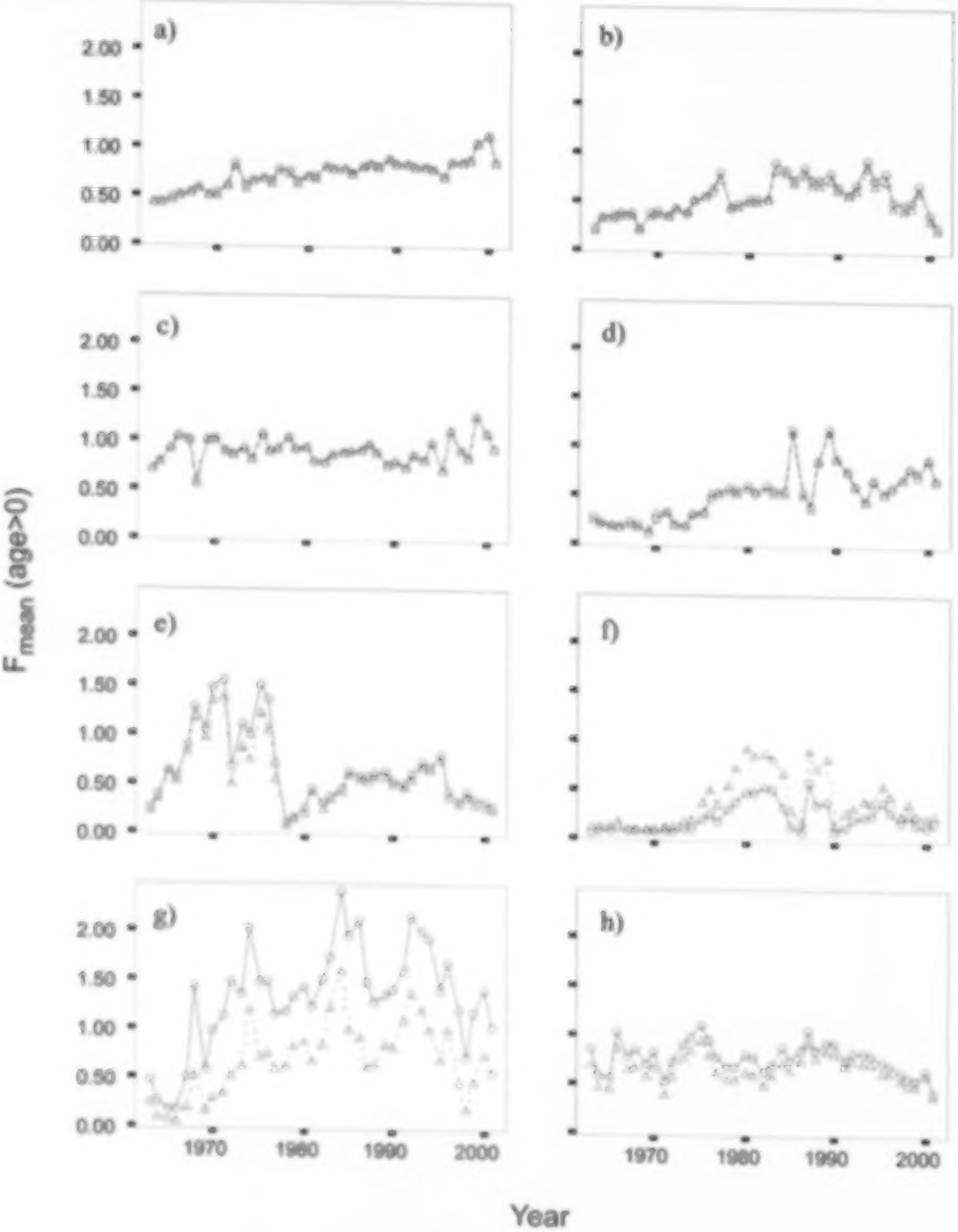
The observed distinctions in SRRs and predation pressures between run 81 and run 91 translated into different predicted SSB developments in midterm forecasts (Fig. 8). The SSB of cod showed a slightly increasing trend in run 91 (59×10^3 t in 2010), whereas in run 81, the trend was slightly negative (27×10^3 t in 2010). When simulating changes in the North Sea food web between hindcast and

Fig. 6. Comparison of multispecies virtual population analysis hindcast results between run 81 and run 91 according to spawning stock biomass (SSB): run 81, line with circles; run 91, broken line with triangles. Graphs are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) saithe (*Pollachius virens*), (*c*) haddock (*Melanogrammus aeglefinus*), (*d*) sandeel (*Ammodytes* spp.), (*e*) Atlantic herring (*Clupea harengus*), (*f*) European sprat (*Sprattus sprattus*), (*g*) Norway pout (*Trisopterus esmarkii*), and (*h*) whiting (*Merlangius merlangus*).



prediction time period in the same magnitude as observed in the field between 1981 and 1991 (run 8191 and run 9181), it became obvious that the choice of the SRR had a strong influence on predicted cod stock developments. Using the SRR of run 81 always led to small decreasing trends in predicted SSB, whereas the run 91 SRR enhanced the recovery potential of cod regardless of the simulated condition of the North Sea food web. However, the level of predation pressure worsened or improved the situation for the cod stock. A real recovery of cod occurred only when the run 91 SRR was combined with predator preferences and prey availabilities of the 1981 food web (run 9181).

Fig. 7. Comparison of multispecies virtual population analysis hindcast results between run 81 and run 91 according to annual mean fishing mortality coefficients (F_{mean}) for ages > 0: run 81, line with circles; run 91, broken line with triangles. Graphs are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) saithe (*Pollachius virens*), (*c*) haddock (*Melanogrammus aeglefinus*), (*d*) sandeel (*Ammodytes* spp.), (*e*) Atlantic herring (*Clupea harengus*), (*f*) European sprat (*Sprattus sprattus*), (*g*) Norway pout (*Trisopterus esmarkii*), and (*h*) whiting (*Merlangius merlangus*).



For whiting, the differences were even more pronounced. In run 81, the SSB was predicted to remain on an almost stable level (214 × 10^3 t in 2010), whereas in run 91, whiting was driven to extinction until 2010. When mixing the input data (run 8191 and run 9181), SSB trends changed again. The SRR and fishing mortalities of run 91 together with the run 81 suitability matrix (run 9181) led to a clearly increasing trend of whiting SSB up to 441 × 10^3 t in 2009. As de-

Table 4. Parameters of the Ricker stock–recruitment curves for the various species included in the model runs (output from 4M).

Species	α	β	α CV	β CV
Run 81				
Atlantic cod	8.43	1.71×10^{-9}	0.326	0.925
Haddock	165.81	6.70×10^{-10}	0.225	0.567
Atlantic herring	63.79	2.96×10^{-10}	0.247	0.678
Norway pout	568.69	1.78×10^{-9}	0.317	0.868
Saithe	2.84	3.26×10^{-9}	0.183	0.217
Sandeel spp.	1197.82	9.75×10^{-10}	0.180	0.212
European sprat	219.90	3.94×10^{-10}	0.198	0.388
Whiting	56.98	2.40×10^{-10}	0.252	2.576
Run 91				
Atlantic cod	64.35	2.09×10^{-9}	0.403	0.936
Haddock	205.59	1.29×10^{-9}	0.229	0.386
Atlantic herring	45.35	8.54×10^{-10}	0.178	0.182
Norway pout	817.44	4.31×10^{-10}	0.208	0.723
Saithe	2.84	3.26×10^{-9}	0.183	0.217
Sandeel spp.	2624.21	1.15×10^{-9}	0.251	0.268
European sprat	422.44	4.50×10^{-10}	0.219	0.611
Whiting	143.32	1.15×10^{-9}	0.256	0.447

Note: CV, coefficient of variation.

scribed before, run 91 led to the extinction of whiting until 2010. So differences in predator preferences and (or) spatial predator–prey overlap as observed between 1981 and 1991 had the potential to reverse future SSB trends of whiting, mediated by the inserted SRR and future fishing mortalities.

A similar influence of the chosen stomach data set emerged for Norway pout and sandeel. For haddock, however, neither differences in the stomach data nor differences in the SRRs could avoid the extinction of haddock in the model until 2010. For herring, run 81 resulted in a strong increase in SSB, whereas run 91 predicted a total collapse until 2010. The mixing of the input data led to a result between the two extremes. The same picture can be drawn for sprat. For this species, however, run 81 simulated the unfavourable conditions.

Discussion

Influence of sampling errors and biases

In this paper, one main focus was on assessing differences in the diet selection of predators and (or) the availability of prey species from two different sets of stomach content data sampled in 1981 and 1991. Respectively, changes in suitability coefficients and consumed "other food" were a direct consequence of the stomach contents reflecting either real changes in the North Sea food web or sampling errors. For cod, whiting, and haddock, the number of sampled stomachs was sufficiently high in both years to reliably deduce their diet composition (Daan 1989; Hislop et al. 1997).

For saithe, the numbers were smaller than for the other gadoids included in the model (3420 stomachs in 1981 and 3219 stomachs in 1991). Although too low numbers of sampled stomachs could lead to random changes between run 81 and run 91, the observed systematic changes in suitability coefficients and the amount of "other food" consumed especially can not be explained by them. Only a sampling bias could lead to such systematic changes. Because it was a declared aim in 1991 to repeat the 1981 stomach sampling project for analysing changes in suitability coefficients over time, a systematic bias (e.g., owing to systematically different sampling coverage in space and time) was avoided as far as possible (Hislop et al. 1997). The spatiotemporal coverage of stomach samples for cod, whiting, and haddock was considered as adequate for both years (Daan 1989; Hislop et al. 1997). The area from where stomach samples are available differed only to a minor extent. The median of the proportional difference in the number of ICES rectangles with stomach data available per ICES roundfish area between 1981 and 1991 was under 20% for three of the four predator species (cod, median = 14%; whiting, median = 14%; haddock, median = 19%). These figures are even overestimates, as situations are also included in which predators of one species were simply absent in one or the other year, i.e., not available for sampling. For saithe, less complete coverage was achieved in both years (Daan 1989; Hislop et al. 1997). However, this just reflects the more patchy distribution of saithe because of shoaling.

In conclusion, random changes in suitability coefficients and the amount of "other food" consumed could to some extent be a result of low sample sizes in one or the other interaction. The systematic changes observed, however, are more likely to reflect real changes in the North Sea food web.

Model vs reality

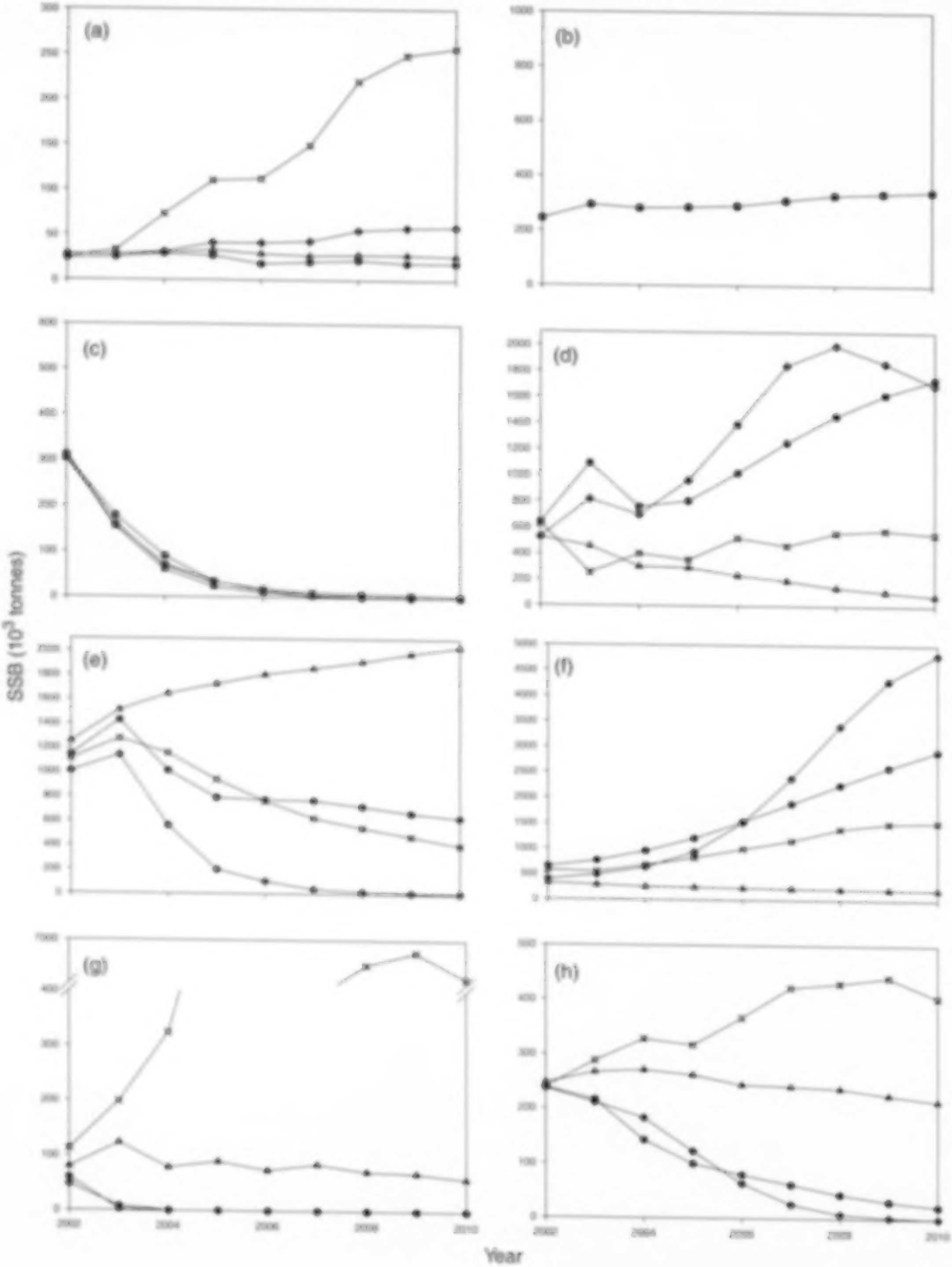
The second main focus of this paper was the quantification of parameter uncertainty in current multispecies assessment methods. This quantification was based on the comparison of two different model runs having all input parameters identical except the input stomach data set.

The absolute values calculated in each run are not expected to match reality. The result of this study that suitabilities vary over time implies that the use of either the run 81 or run 91 suitability matrix for the entire calculation time period must lead to unrealistic results for at least parts of the historic and future time series. However, in this study only the relative differences between the model runs were of interest. The observed differences between run 81 and run 91 directly reflect the magnitude of diet data related parameter uncertainty in current North Sea multispecies assessment.

Absolute changes in suitabilities

The assumption of time-invariant suitability coefficients is one of the most important hypotheses in MSVPA and MSFOR theory (Sparre 1991; Magnusson 1995). In the current study, mainly small absolute differences between the 1981 and 1991 suitability matrices were observed. In some interactions, however, pronounced differences were found. Absolute differences can reach values of up to ±0.8 at a theoretical maximum of one. This result is in line with analyses by the MAWG on suitability changes between 1981 and 1991 made with input data of key runs 1993 and 1997 and the same predator and prey species included in the model runs (ICES 1994, 1997). The MAWG stated that according to suitability changes the "similarities are greater than the differences" (ICES 1997) because the predominant fraction of suitability changes is small in absolute terms. However, it

Fig. 8. Predicted spawning stock biomass (SSB) development resulting from runs 81 (—▲—), 91 (—◆—), 8191 (—●—), and 9181 (—×—). Stock developments are shown for (*a*) Atlantic cod (*Gadus morhua*), (*b*) saithe (*Pollachius virens*), (*c*) haddock (*Melanogrammus aeglefinus*), (*d*) sandeel (*Ammodytes* spp.), (*e*) Atlantic herring (*Clupea harengus*), (*f*) European sprat (*Sprattus sprattus*), (*g*) Norway pout (*Trisopterus esmarkii*), and (*h*) whiting (*Merlangius merlangus*).



can be shown that absolute suitability changes are not a good measure of the importance of observed suitability changes. Suitability coefficients are calculated as the ratio of the relative stomach content of a certain prey to the biomass of this prey in the sea. Because of this calculation method, suitability coefficients from interactions with prey species and prey age groups that have high prey stock biomasses can be small in both suitability matrices even if the contribution of a certain prey species to the diet of a certain predator is high. This mechanism leads to comparatively small absolute suitability changes, although the proportional differences and the impact on model results might be serious (e.g., interaction between fourth-quarter age-2 whiting and age-0 Norway pout: suitability coefficient run 81 = 0.02, suitability coefficient run 91 = 0.124, absolute difference = 0.1, relative difference = 531%). Therefore even small absolute suitability changes can stand for important and highly influential changes in predator preferences and (or) spatial predator–prey overlap. On the other hand, high suitability changes do not necessarily lead to large differences in the calculation of stock abundances. Because the interpretation of suitability coefficients is not straightforward, the effect of the observed suitability changes on model results and so on the inherent uncertainties of current multispecies fish stock assessment will be discussed on the basis of easier-to-interpret differences in historic and predicted stock biomasses between runs 81 and 91.

Systematic shifts in the North Sea food web

Often all predator age groups of a certain predator species showed suitability changes in the same direction for a particular prey species. For example, whiting in all predator age groups exhibited a considerably stronger tendency towards cannibalism in the first quarter of 1991 than in 1981. The emergence of such patterns can be seen as a hint that underlying processes affected all predator age groups in the same way.

Prey switching and a variable spatial overlap between predator and prey populations are discussed as potential processes leading to such systematic changes in suitabilities over time (Hilden 1988; Magnusson 1995). Prey switching means that suitabilities depend on prey abundance, in contrast to the present suitability concept. Prey switching in MSVPA was analysed earlier: Rice et al. (1991) observed a tendency towards positive prey switching in an analysis of suitability changes between the stomach years 1981 and 1985 to 1987. In contrast, Larsen and Gislason (1992), ICES (1994), and Rindorf et al. (1998) observed a tendency towards negative prey switching by analysing suitability coefficients calculated from the 1981 and 1991 stomach data. The analyses carried out to date on this topic were only able to explain the observed suitability changes between 1981 and 1991 to a minor extent and were controversial in their results.

The mentioned analyses, however, did not take into account changes in predator–prey overlap as an alternative explanation for suitability changes. Spatial overlap is a function of the abundance of both predator and prey (Marshall and Frank 1994; Shepherd and Litvak 2004) but can also vary because of environmental and climatic changes. Many authors have demonstrated the dependence of fish distribution on climatic and hydrographic factors for different species in different regions of the North Atlantic (e.g., Corten 1990; Jones and Hislop 1978; Murawski 1993). Preliminary results (A. Kempf, unpublished data) show that the performance of the MSVPA diet selection model in predicting relative stomach contents can be significantly improved by taking into account variable spatial predator–prey overlap. As an example, International Bottom Trawl Survey (IBTS) data suggest that the spatial overlap between 1-year-old whiting and older (age 2+) whiting substantially increased between 1981 and 1991 (e.g., first-quarter Williamson (1993) overlap index whiting age 4 with whiting age 1: 1981 = 0.83, 1991 = 2.02). This potentially explains the already mentioned stronger tendency towards whiting cannibalism in 1991.

Therefore, further analyses on suitability changes, including all underlying processes (e.g., overlap and prey switching), must be carried out. The Working Group on Multispecies Assessment in the Baltic (WGMAB) suggested a new procedure for averaging suitabilities when more than one stomach data year is available (ICES 1992*b*). Although some of the random differences between observed and predicted relative stomach contents were reduced with this method, systematic changes via processes not included in the diet selection model were still not taken into account. Because of the calculation procedure, it becomes obvious that suitability coefficients are a "black box" parameter and changes in suitabilities come from the sum of all influences (prey switching, overlap). A complete new formulation of the diet selection model will be needed to allow for the use of overlap coefficients and a separation of the processes responsible for systematic changes in suitabilities.

Changes in the amount of "other food" consumed occurred as an additional shift in the North Sea food web, e.g., cod, whiting, and saithe substantially consumed less "other food" in 1991 than predicted by the currently implemented MSVPA diet selection model. This means, in turn, that in reality more of the so-called MSVPA prey species (e.g., cod, whiting, Norway pout, sandeel) were consumed by these predators in 1991 than predicted by the Holling type II functional feeding response implemented in the model.

If the assumption of a constant "other food" biomass in the sea is valid, then the observed deviations between predictions and observations would translate into either a strong negative prey switching for all mentioned predator species (more MSVPA prey species were eaten in 1991 than in 1981, although the total biomass of MSVPA prey species was lower in 1991) or the overlap between MSVPA prey species and predators being higher in 1991. However, a third possibility is more likely. The regime shift around 1987 was characterized by changes in the species composition of zooplankton (Reid et al. 2001*a*; Beaugrand and Reid 2003) and benthic communities (Reid and Edwards 2001), representing a large part of "other food" found in the stomachs (Daan 1989; Hislop et al. 1997). This change may have led to a decrease of "other food" species preferred by the predators. For example, euphausiids were an important prey species for saithe in 1981. In the 1991 stomach data, significantly less euphausiids but increased amounts of herring and Norway pout were found in the stomachs (Anonymous 1998). After the regime shift in the late 1980s, warmer water temperatures tended to prevail in the North Sea (Beaugrand and Ibanez 2004) and the cold water adapted euphausiids were observed to decrease in abundance (Beaugrand et al. 2003; Beaugrand 2004). For comparison, the same shift in the diet of saithe was found on the Scotian shelf where a significant decrease of euphausiids found in the stomachs was observed for the years 1996–2002 in contrast to earlier stomach samples from 1958 to 1967 (Carruthers et al. 2005).

Therefore, treating "other food" as a single prey type is a major simplification that affects the model performance. An enhancement of the model may be to split "other food" into more categories to account for changes in the species composition.

Uncertainties in model results and their implications for fish stock assessment

The changes in suitability coefficients and the amount of "other food" consumed between 1981 and 1991 led to differences in hindcast results of run 81 and run 91. The trajectories of SSBs and fishing mortalities, however, were generally weakly influenced, except for those of Norway pout. This reflects the fact that, for a number of species, predation mortalities of age groups contributing mainly to the SSBs and catches are low. However, in contrast, the high similarity of sandeel SSBs in both runs was caused by complex second-order multispecies effects. For example, in whiting as the main predator for sandeel, lower relative stomach contents of sandeel in the 1991 stomach data set were found, decreasing the predation pressure on sandeel in run 91 compared with run 81. On the other hand, higher whiting stock numbers were calculated in run 91, increasing the predation mortality on sandeel. Both processes almost compensated for each other, contributing to the observed similarity of calculated historic sandeel SSBs.

For 0-group recruits of all species and for the SSB of Norway pout, a species in which all age groups receive high predation pressures, the effect of differences in predation levels were more pronounced. The calculated recruitment numbers in run 91 were clearly higher than in run 81 for all species analysed (recruitment estimates are up to 1474%, 1091%, 494%, and 283% higher for cod, Norway pout, sandeel, and whiting, respectively, in run 91 than in run 81). The shift of parts of their diet from "other food" towards MSVPA prey species in 1991 led to an increase of MSVPA fish prey stock numbers in the backward MSVPA calculations of run 91. Suitability changes between 1981 and 1991 generating different predation pressures and second-order multispecies effects are other processes that led to differences in recruitment estimates.

Overall, temporal trends and magnitudes of SSBs and fishing mortality estimates, important parameters for fisheries management, were rather robust towards changes in the diet data model input. In a former analysis of the MAWG, the MSVPA stock trajectories were correlated with IBTS survey indices and matched the average populations well (ICES 1994), underlining that MSVPA calculations are generally valid. For 0-group recruits, however, the correlations tend to be lower (Kempf et al. 2005), which is thought to reflect the higher uncertainties for 0-group fish in the model and, because of lower catchabilities, in the survey. Also, in this study, most uncertainties are related to the calculation of 0-group recruits. The use of different diet data sets led to differences in recruitment numbers and their trajectories, which translated into different Ricker SRRs.

These uncertainties in MSVPA calculations became especially obvious when predicting future SSB developments, where the survival rate of 0-group recruits is an important driving force. Our study demonstrates that top-down effects mediated by changes in predator preferences and (or) spatial predator–prey overlap, as well as changes inside "other food", can lead to major changes in modelled and real recruitment success. The number of 0-group survivors at different predation pressures, mediated by the condition of the food web, determined the predicted stock development to a large extent. Differences in stock–recruitment relationships calculated in run 81 or run 91 (e.g., whiting, Norway pout, and sandeel) had only a modulating influence. Even the effects of an eightfold increase in the Ricker α coefficient for cod in run 91 were overruled by top-down food web effects, which substantially determined the recovery potential of cod. The typical fisheries management question, whether fish stocks will increase or decrease at a given fishing mortality and stock–recruitment relationship in the near future, can easily be answered in opposite directions for a number of species (e.g., whiting, sandeel) just by altering the assumption on the condition of the North Sea food web from the 1981 to the 1991 status and vice versa.

Future perspectives

The North Sea ecosystem has been subjected to further changes since 1991. The gadoid stocks have further declined, whereas clupeid stocks have shown increasing trends (ICES 2004, 2005*b*). The stocks of the most important prey species, Norway pout and sandeel, have declined dramatically in recent years (ICES 2005*b*). In addition, species with southern geographic affinities have increased in abundance (Beare et al. 2004), and predators of little commercial relevance, such as grey gurnard, are discussed to exert high predation pressure, especially on juvenile gadoids, filling niches in the food web (Floeter et al. 2005). Also, further climatic changes have been observed since 1991, e.g., water temperatures have increased further (Beare et al. 2004). Therefore it is highly probable that the North Sea food web has further advanced to stages not covered by available diet data sets and that neither run 81 nor run 91 reflects the current ecosystem status. Unrealistic results such as the predicted extinction of haddock until 2010 in all runs are further hints towards an unknown food web status not covered by the available data sets. Our process understanding is not yet sufficiently advanced to predict it from the 15- to 25-year-old stomach data. For parameterizing and testing new diet selection models, as well as being able to take into account the current food web status in assessment models, a current update of the stomach data time series is necessary, at least until our process understanding allows robust predictions of the future predation mortalities.

The recent decline of cod, sandeel, and Norway pout stocks in the North Sea (ICES 2005*b*) underlines the need for a change in the current fisheries management approaches, a change that would take into account to a greater degree environmental variability and biological processes.

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